RETENTION OF THREE TAXA OF POSTLARVAL FISHES IN AN INTENSIVELY FLUSHED TIDAL ESTUARY, CAPE FEAR RIVER, NORTH CAROLINA

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ABSTRACT

Fixed nets were used to sample postlarvae of spot, *Leiostomus xanthurus*, Atlantic croaker, *Micropogonias undulatus*, and flounders, *Paralichthys* spp., over several 24-hour periods in the Cape Fear River, near Wilmington, North Carolina. Results of analyses of variance on abundance data collected at two locations indicate that these taxa exhibit distinct behavioral responses, primarily to photoperiod and tide, which allow them to maintain a selected position in the estuary and avoid being flushed seaward. The level of response to these variables dictates ultimate residence in at least two primary nurseries, the river main stem in the vicinity of the salt boundary and the tidal salt marshes. By migrating to the surface at night, both spot and flounders make apparent use of tides to augment lateral migration into marshes. Conversely, by tending to remain more bottom oriented at all times, Atlantic croaker accumulate in greater numbers in deep water at the head of the estuary.

Mechanisms by which larval fishes are recruited to, and concentrated in, estuaries are poorly understood. Attempts to elucidate these mechanisms suffered from the generally high degree of variability associated with sampling larval fish populations. Recognizing this, Graham (1972) employed fixed nets to collect larval Atlantic herring, *Clupea harengus*, in the Sheepscot estuary of Maine. His gear offered the advantage of obtaining synoptic samples over the entire water column, and because much greater volumes were filtered, the variability of the data was also reduced. Consequently, he was able to infer a mechanism used by Atlantic herring larvae to select a specific reach of the estuary, i.e., a behavioral response manifested by interactions between depth, or location, and tidal direction.

The importance of such interactions has not always been fully appreciated; e.g., Pearcy and Richards (1962) postulated that larval fish transport in the Mystic estuary occurred mainly in the lower layer by net nontidal flows. Similarly, Haven (1957) and Sandifer (1975) described utilization of net nontidal transport in the lower layers for fishes and invertebrates in the Chesapeake Bay. However, these investigators collected larvae during the daytime only and did not consider diel migrations which may bring many larvae to the surface at night (Pacheco and Grant 1968; Lewis and Wilkens 1971; Williams and Porter 1971). Moreover, certain larval fishes (e.g., menhaden) may also frequent the upper layers to a considerable extent during the day (Thayer et al. in press). Thus, it is probable that the retention mechanism is species-specific and involves several elements as described by Bousfield (1955): 1) diel changes in vertical distribution; 2) utilization of the residual, or nontidal, drift seaward in the upper layer and landward along the bottom; and 3) changing behavioral parameters with respect to tidal direction (e.g., see also Hughes 1969a, b, 1972; Turgeon 1976). Individual species may utilize one or more of these mechanisms to reach and stay within a preferred zone of the estuary, from its mouth (Carriker 1951) to the headwaters (Haven 1957; Turgeon 1976).

Here we describe distributions of postlarval fishes in two locations within the Cape Fear River estuary, near Southport, N.C. Both sampling areas were situated upriver, in an area believed to constitute a primary nursery zone for several fish species. Sampling was stratified by location, depth, photoperiod, and tidal direction, and an attempt was made to depict postlarval fish behavior with respect to these strata. A hypothesis is

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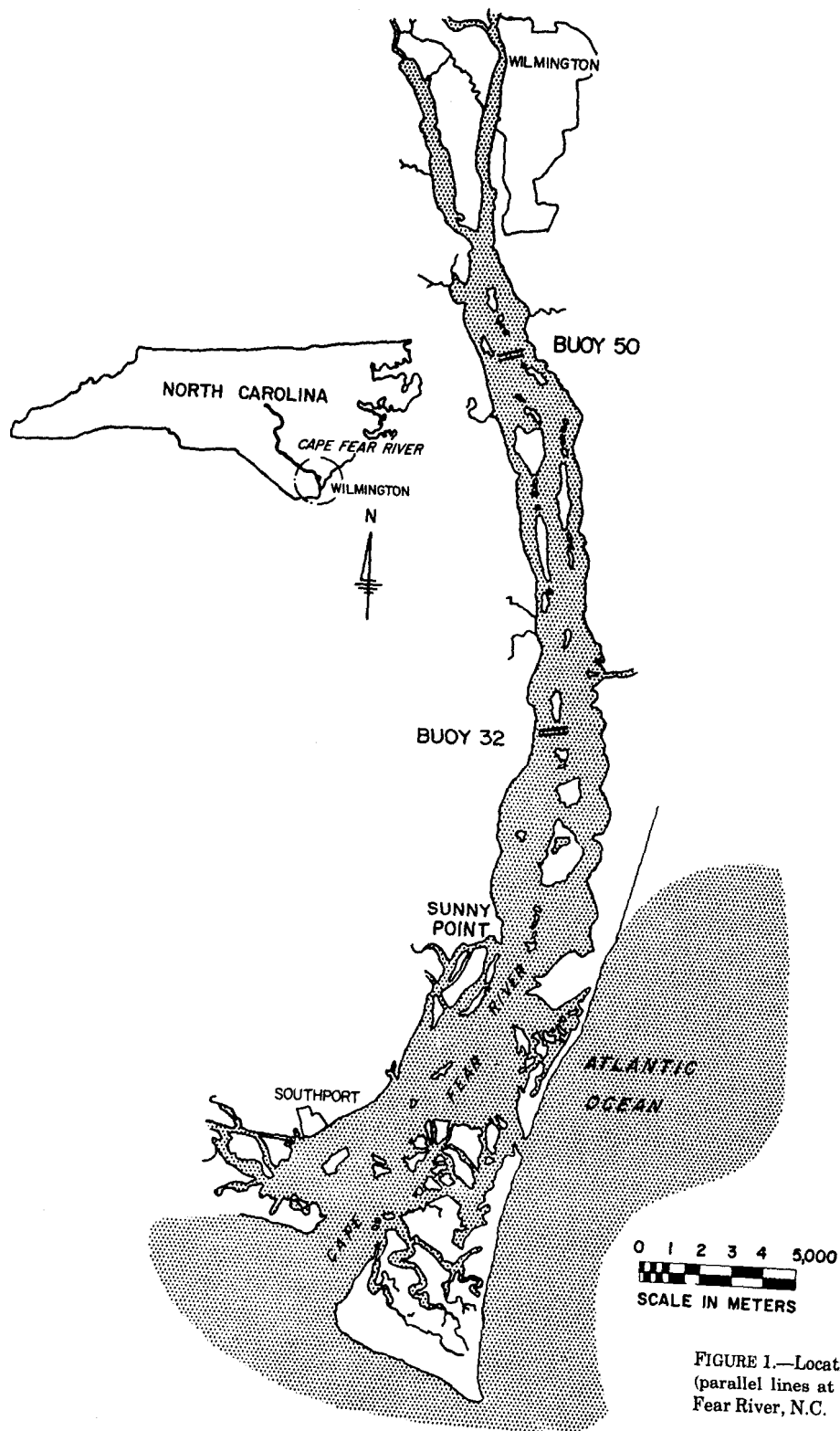[3]Department of Zoology, North Carolina State University, Raleigh, NC 28603.

FIGURE 1.—Location of sampling transects (parallel lines at bouys 32 and 50), Cape Fear River, N.C.

formulated which relates these behavioral responses to the maintenance of a preferred position within the estuary.

STUDY AREA

The Cape Fear River estuary (approximately lat. 33° N) is relatively narrow, averaging only 1.6-3.6 km in width and extending 45 km from the general location of the salt boundary at Wilmington, N.C., to the river mouth at Baldhead-Smith Island (Figure 1). A 12 m deep ship channel with a width of 120-150 m is maintained from Wilmington to the river entrance, and adjacent spoil islands are found along its entire length. Tidal velocities in the Cape Fear are high, averaging 2.1 m/s during ebb near the city of Southport, N.C. (National Ocean Survey 1977). Recent hydrographic and dye studies (Carpenter[4]) have established that a two-layer system occurs in the

estuary between the vicinity of Sunny Point and Wilmington (Figure 1).

Extensive tidal salt marshes cover about 8,900 ha and form the largest contiguous system of this type in the State of North Carolina (U.S. Army Corps of Engineers[5]). Tidal creeks cover an estimated 648 ha, and shallow open water areas (shoals) between the channel and salt marshes contribute an additional 7,285 ha of suitable nursery habitats for the young of fishes and shellfish.

MATERIALS AND METHODS

A modified version of the gear designed by Graham (1972) was employed in this study (Figure 2A). Individual 0.5 m plankton nets with stainless steel cod end buckets were suspended from aluminum collars (Figure 2B) and bolted onto orienting vanes attached to a 9.5 mm diam-

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[4]Carpenter, J. H. 1979. Dye tracer and current meter studies, Cape Fear Estuary 1976, 1977 and 1978. Final report to the Carolina Power & Light Co., Raleigh, N.C., 339 p.

[5]U.S. Army Corps of Engineers. 1977. Maintenance of Wilmington Harbor, North Carolina. Final environmental statement. U.S. Army Engineers District, Wilmington, N.C., 97 p.
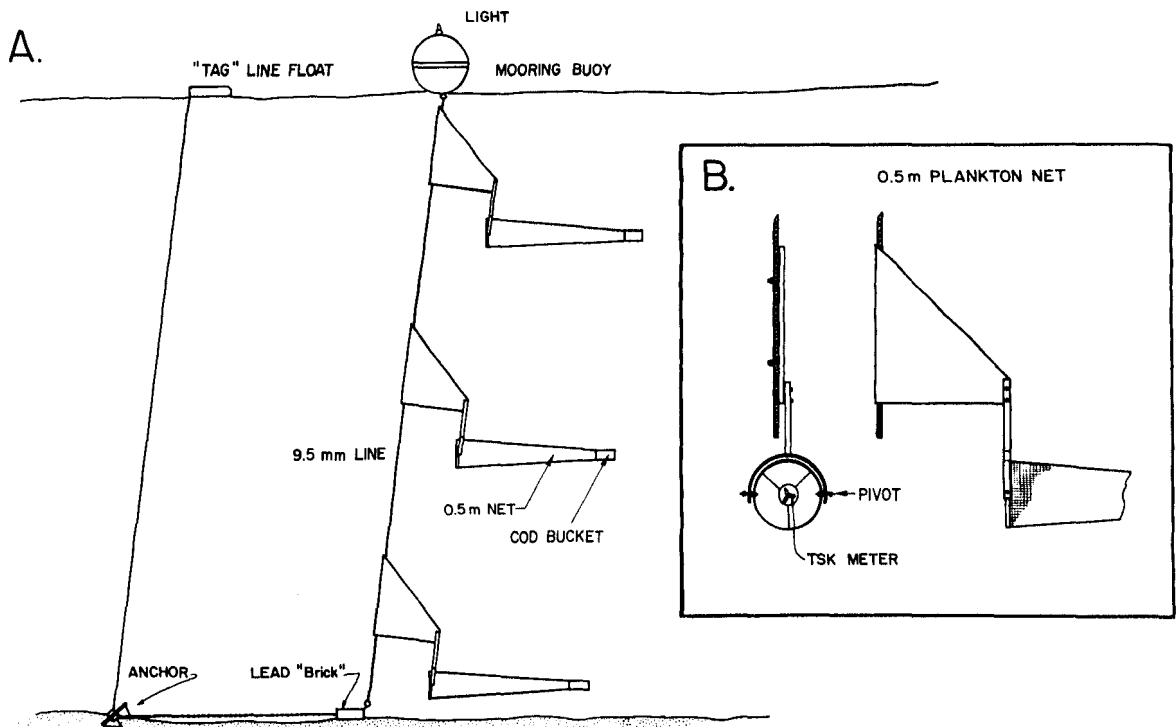

FIGURE 2.—A. Sampling apparatus and deployment, the middepth nets were not used on the east and west shoals. B. Detail of the orienting vane and net mounting. Paired meters were used on all bottom nets.

eter nylon rope. Tidal flows in the Cape Fear estuary were sufficiently high to fully extend these nets during the sampling period. Lead weights (66 kg) between the anchor and bottom net were used to fix the depth at which the bottom nets fished, and a tag line and float attached to the anchor shaft allowed each rig to be easily retrieved at the end of the sampling period. Surface nets were rigged to sample at 1.5 m below the surface, mid-depth nets at a depth of 6.5 m (in the main channel), and bottom nets, approximately 1 m above the substrate. In order to reduce detection by post-larvae, all nets were dyed deep brown (Rit[6] #20, Cocoa Brown—W. Watson[7]).

Samples were collected at two locations on three sets of dates: 14-15 March, 5-6 April, and 11-12 April. A pair of closely spaced transects were situated near river buoy 50, close to the head of the estuary, and another pair at river buoy 32, at Snow's Cut (Figure 1). Two vessels were employed on each sampling date, and for each transect, three stations were established across the main channel from east to west. At slack water the east and west shoal rigs were set first in 7.6 m of water, and the channel station nets were anchored last. All nets at each of the paired transects were set in <40 min. Because the period of slack water continued for the duration of the setting process, the nets actually began to fish simultaneously and, except for the period of retrieval (about 20 min), a nearly synoptic set of samples was taken across a cross section of the main channel and shoals. On each pair of dates four consecutive tides were sampled, with nets retrieved after 2 h. Limiting the sampling period to 2 h was a necessary precaution in this study because of the potential for net clogging in the highly turbid Cape Fear estuary (see below).

It was planned to sample two nighttime and two daytime tides during each survey but, due to differences in the predicted and actual tides, there was sufficient ambient light to read field data sheets by the end of the last night set at buoy 50 on 6 April. For this reason, the sample was excluded from the analyses.

To reduce the potential for clogging, nets were constructed of 752 μm mesh material and tapered to a length of 3 m. Meshes of this size allowed the

passage of many small plankton as well as fine detritus, but retained the postlarvae [≈7-34 mm SL (standard length)] of interest. Previous studies of comparative length frequency in 505 and 760 μm nets (Copeland et al.[8]) indicated that postlarvae <7 mm (of the species of interest) were uncommon in the Cape Fear estuary, since they were recruited from well offshore.

In a preliminary experiment in November 1976, five nets were fished near the bottom, off a tidal creek bridge, and pulled sequentially every 0.5 h after an initial fishing period of approximately 1.0 h (Table 1). The flow past each net was monitored by a TSK[9] meter mounted in the center of the mouth of each net and by a second meter affixed to the collar support. After more than 3 continuous hours of fishing at relatively low flows (compared with the main channel), clogging, as determined by the difference between the inside and outside meter readings, did not exceed 28% on the last net pulled. However, a piece of filamentous algae was found wrapped around the inner TSK prop and axle on this net, restricting free movement. Meter fouling caused by fibrous detritus and algae along the river bottom created considerable difficulties in obtaining useful bottom meter readings in the actual experiments and was deemed a more serious problem than severe net clogging.

In an attempt to overcome bias due to fouled meters, all bottom nets were fitted with paired TSK meters as described above. Based upon the results of the preliminary study (Table 1), it was conservatively estimated that an inside meter

[8]Copeland, B. J., R. G. Hodson, and R. J. Monroe. 1979. Larvae and postlarvae in the Cape Fear River estuary, North Carolina, during operation of the Brunswick Steam Electric Plant, 1974-78. Report 79-3 to Carolina Power & Light Co., Raleigh, N.C., 214 p.
[9]Tsurumi Seiki Kosakusho Company.

TABLE 1.—Preliminary net clogging study at Walden Creek, Cape Fear River. Negative percentage difference indicates that inside meter reading was largest.

Net	Time retrieved	Meter	Meter revolutions	Volume (m³)	% difference (inside/outside)
1	1235	Inside	3,053	97	5
		Outside	3,214		
2	1305	Inside	8,633	275	3
		Outside	8,896		
3	1336	Inside	6,822	217	-7
		Outside	6,357		
4	1406	Inside	14,402	458	9
		Outside	15,812		
5	1437	Inside	12,565	¹400	28
		Outside	17,410		

¹A piece of filamentous algae was found wrapped around the TSK prop and axle, restricting free movement.

reading <80% of the outside reading would indicate that the inside meter had fouled. Of the 144 bottom samples collected, 71 had low inside meter readings and 16 had high inside readings. An additional 3 samples were discarded due to gear failure, leaving a total of 54 samples that could be used to obtain an estimator for volume.

A strong linear relationship between inside and outside meter readings ($r = 0.996$, $P<0.01$) indicated that an adequate linear predictor could be obtained:

$$Y = 0.913 \, X$$

where Y is the inside meter reading and X is the outside meter reading, both in revolutions. The standard error of the slope of this line is 0.009, and the standard error of an individual estimate of the inner reading is:

$$SE = \sqrt{7.4729 \times 10^{-5} \, X^2 + 1.758337 \times 10^6} \; .$$

The above estimator was used to obtain volumes for all bottom samples in which the inside meter reading was <80% of the outside reading. If a net were actually clogged when we assumed that the meter was fouled, this procedure would result in an overestimate of the volume filtered and underestimate of the actual density of larvae present. Thus, differences among strata would be even larger than depicted in our data.

Upstream and downstream nets at each depth along the paired transects served as replicates in the experiments. This survey constituted a factorial design, with site, photoperiod, and tidal direction as main effects. Nonorthogonal factorial analyses of variance (ANOVA) (Searle 1971) were performed for each taxon, date, and buoy (except spot and Atlantic croaker at buoy 50 on 14-15 March). Examples of the analytical results are reproduced in Appendix I to allow the reader to follow our procedures. A posteriori multiple comparison procedures (Bonferroni t-tests $\alpha = 0.05$; O'Neill and Wetherill 1971) were used to examine station and depth differences and their interactions with photoperiods and tides. Prior to analysis, data were logarithmically transformed [$\log_{10} (10 + X)$] in order to meet the homoscedasticity requirement of ANOVA.

A partial data analysis was performed for 5 April 1978 at buoy 50, deleting the last night set. Either daytime or ebb data alone were used, depending on the strata compared. However, data from all three valid sets were used to obtain an estimate of sampling variability.

All collections were preserved in 5% buffered Formalin, and selected taxa were enumerated and measured for standard length (SL). The latter measurement was taken from the tip of the snout to the end of the notochord or hypural plate. Subsampling for lengths was employed when sorted collections contained >100 individuals of a given species. Data are presented herein on three taxa: spot, *Leiostomus xanthurus*; Atlantic croaker, *Micropogonias undulatus*; and flounders of the genus *Paralichthys*. Flounders were counted but not measured in this program.

RESULTS

Since the April sampling dates were near the end of recruitment for winter-spawned species in the Cape Fear estuary, the observed pattern of distribution during this month should reflect the selection of preferred nursery habitats. On 14-15 March, freshwater flow in the river exceeded 990 m³/s, and the salt boundary was below buoy 50, as indicated by the absence of measurable salt in the water column. On these dates, spot were entirely absent at buoy 50 and only two Atlantic croaker postlarvae were captured (Figures 3, 4). Flounders, however, were abundant at buoy 50 during this period. When subsequent sampling indicated that the salt front was restored to its normal location, about 6 km above buoy 50, catches of all taxa (with one exception) were significantly greater ($P<0.05$) upstream (Table 2).

Diel Behavior

Significant differences were only occasionally detected among stations and were likely influenced by local patterns of current and larval transport. For this reason, these comparisons were not considered further and were omitted from the ANOVA summary (Table 3). Consistant trends, however, were evident in several other comparisons involving depth, photoperiod, and their interactions. For example, the 24 h mean abundance across depths for spot and Atlantic croaker, and to a lesser degree for flounders, was higher (see also Figures 3, 4) at the bottom on the shoals and at middepth and below in the channel, with essentially no differences between buoys. Photoperiod, on the other hand, influenced the catches of flounder in a consistent manner. Except for 14-15
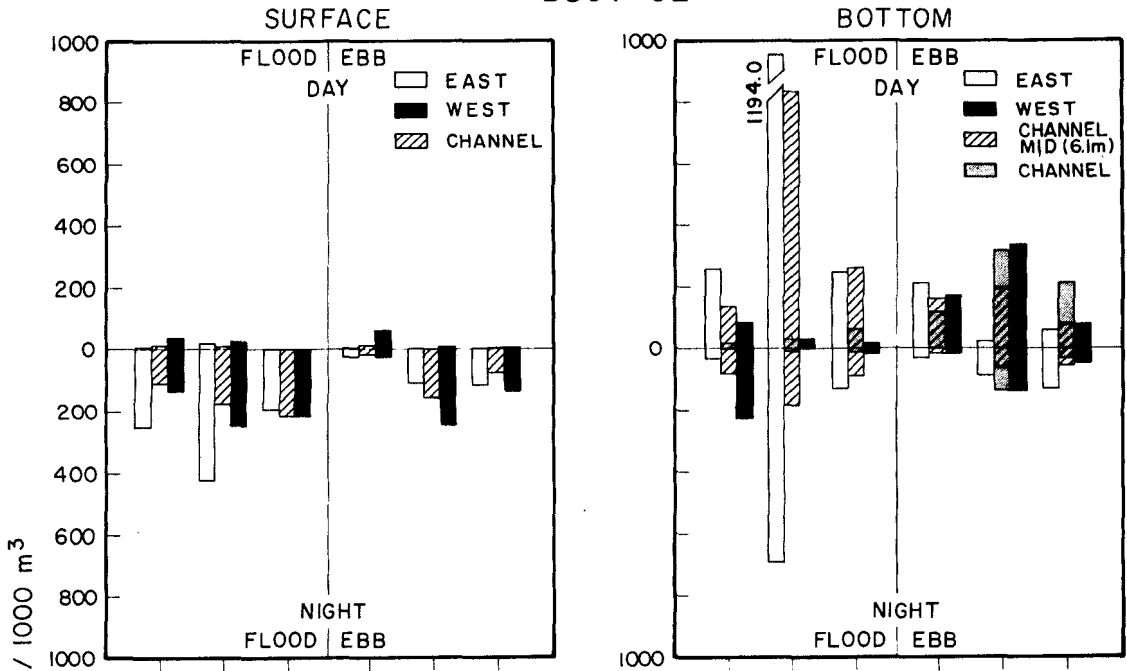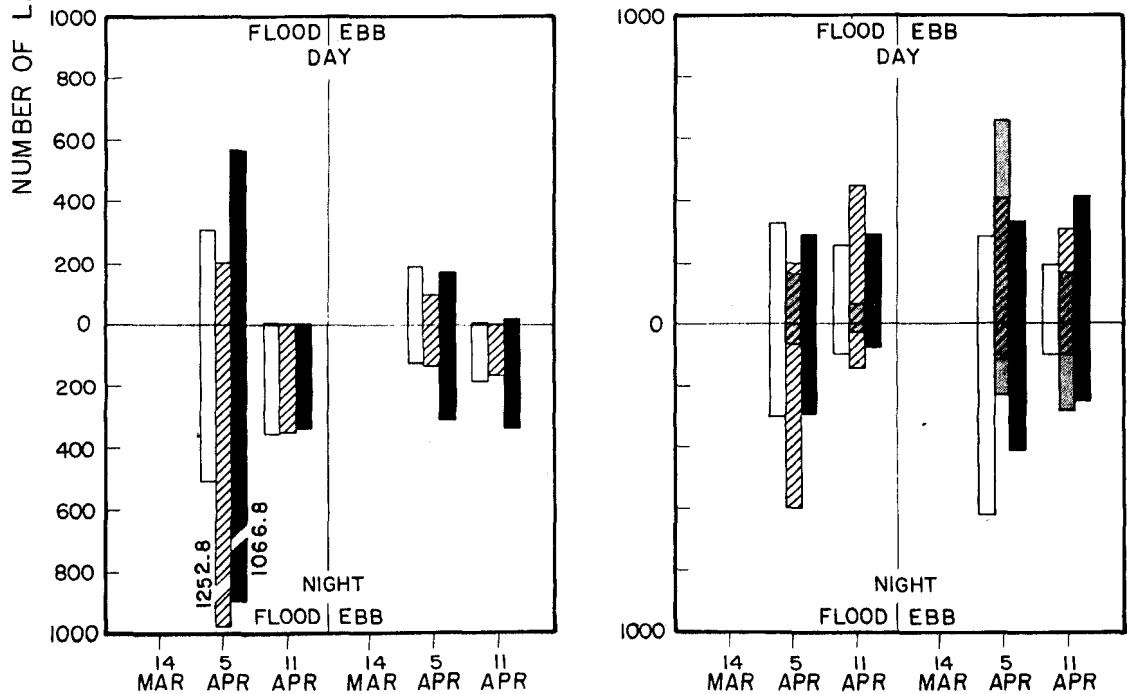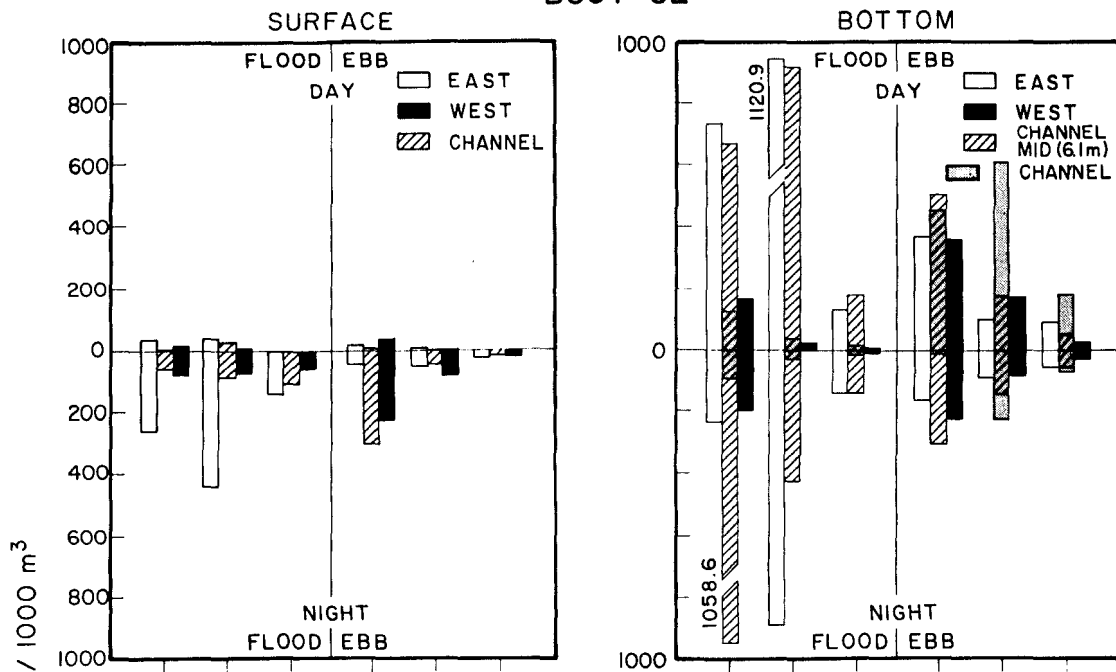
FIGURE 3.—Abundance of spot, *Leiostomus xanthurus*, collected on three sampling dates at buoys 32 and 50. Data are stratified to show mean values for each paired transect with respect to surface-bottom, day-night, and flood-ebb catches. Spot were not captured at buoy 50 on 14-15 March.
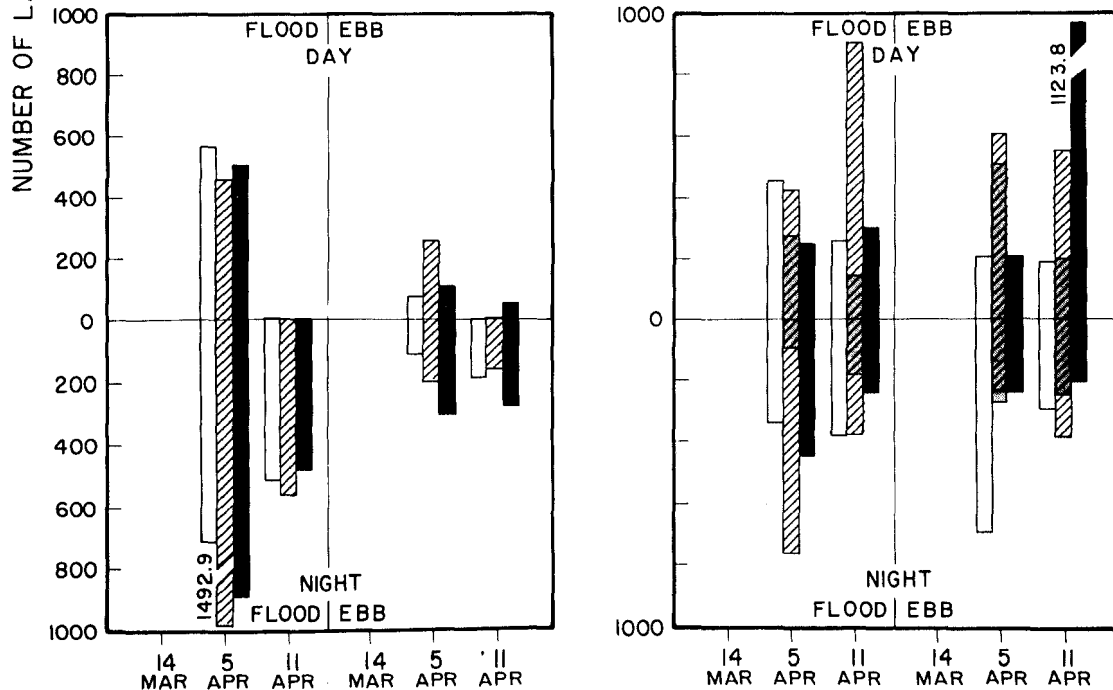
FIGURE 4.—Abundance of Atlantic croaker, *Micropogonias undulatus*, collected on three sampling dates at buoys 32 and 50. Data are stratified to show mean values for each paired transect with respect to surface-bottom, day-night, and flood-ebb catches. Only two croaker were captured at buoy 50 on 14-15 March, these are not shown.

TABLE 2.—Comparison of mean density (number/1,000 m^3) at buoy 32 versus buoy 50 for spot, Atlantic croaker, and *Paralichthys* spp.

Date	Spot			Atlantic croaker			*Paralichthys* spp.		
	Buoy	Mean	*t*-value	Buoy	Mean	*t*-value	Buoy	Mean	*t*-value
14-15 Mar.		No analysis conducted					32	46.7	
									14.76*
							50	147.8	
5-6 Apr.[1]	32	193.4		32	189.4		32	17.3	
			7.85*			11.55*			1.40
	50	302.7		50	329.3		50	18.0	
11-12 Apr.	32	89.1		32	52.6		32	2.3	
			8.91*			4.79*			3.64*
	50	179.2		50	294.9		50	3.9	

*Significant at α = 0.05; transformed log(10 + X) data utilizing error mean squares from initial ANOVA's.
[1]Last night set omitted.

March at buoy 50 and 5-6 April at buoy 32, catches at night exceeded those taken during daylight (Table 3). A similar pattern did not emerge for spot and Atlantic croaker, although night values on 11-12 April at both buoys were significantly higher. Apparently, net avoidance was negligible in this study, unlike the findings of Graham (1972), who limited his sampling for larval Atlantic herring to night hours in the Sheepscot estuary because of what he described as excessive daytime net avoidance. High tidal velocities and the turbid waters of the Cape Fear estuary may have been partially responsible for this difference. Flounders were either better able to detect the dyed nets or perhaps exhibited somewhat different diurnal behavior; e.g., a greater tendency to rest on the bottom during the day.

A response to light was further established by an examination of the photoperiod by depth interactions for the three taxa. During the day, spot and Atlantic croaker were most abundant at the bottom and at middepth. Only in the partial data sets analyzed on 5 April 1978 and for Atlantic croaker at buoy 32 on this date was this pattern changed. On this date, depth distributions did not differ for Atlantic croaker and the surface concentration for spot at buoy 50 was not significantly smaller than the channel middepth value. The trend for flounders was similar, although not as distinct as for the other species. At night, all three taxa moved higher in the water column but to differing degrees. Whereas flounders and spot tended to congregate nearer to the surface, most Atlantic croaker remained lower in the water column (Table 3).

Of the five significant photoperiod by depth interactions involving flounders, a posteriori tests conducted for night data indicated that surface concentrations in four instances were significantly greater than at all other depths. Spot also tended to accumulate toward the surface, on the two dates at buoy 32 where a significant interaction was detected, night catches at the surface exceeded those at the bottom; in the main channel, however, surface and middepth concentrations were not significantly different, although the mean for the former always exceeded that of bottom values by a substantial margin.

The best indication of a diel movement by Atlantic croaker occurred in the main channel where the mean for surface night collections diverged less from that of other depths (see also Figure 4), while during the day, the mean for surface collections was usually significantly lower. No surface accumulation was detected for Atlantic croakers on the shoals, on the single date where a significant difference was observed, bottom catches were greater than at the surface.

Response to Tide

Ebb tide catches were generally lower for all taxa than those of corresponding flood tides (Figures 3-5). In addition, a shift in catch density from channel middepth toward the bottom occurred on ebb, and in several instances bottom concentrations exceeded those of middepth nets for all species.

The observed difference between ebb and flood concentrations was always significant for flounders, and on two occasions, for Atlantic croaker. Tide alone did not seem to exert a major influence on the concentrations of spot, although a significant tidal effect was observed on 14-15 March 1978.

All three taxa displayed a trend towards larger flood catches on the eastern shoal and in the channel, while on ebb the western shoal often exhibited

TABLE 3.—Analyses of variance summary, for stations (depths), photoperiod and tides. Station as a main effect is omitted and not all possible interactions are shown. Multiple comparison test results are shown below individual letter designations.

Source	Buoy 32			Buoy 50		
	14 March	5 April	11 April	14 March	5 April[1]	11 April
Depths[2]						
East/west						
Spot	B>S	B>S	B>S	—	(B>S)	B>S
Atlantic croaker	B>S	B>S	B>S	—	(B>S)	B>S
Paralichthys spp.	B>S	ns[3]	ns	ns	(ns)	ns
Channel						
Spot	M B S	M B S	M B S	—	(B M S)	M B S
Atlantic croaker	M B S	M B S	M B S	—	(ns)	M B S
Paralichthys spp.	M S B	ns	ns	ns	(ns)	ns
Photoperiod[4]						
Spot	ns	D>N	N>D	—	(ns)	N>D
Atlantic croaker	ns	D>N	N>D	—	(ns)	N>D
Paralichthys spp.	N>D	D>N	N>D	ns	(N>D)	N>D
Tides[5]						
Spot	F>E	ns	ns	—	(ns)	ns
Atlantic croaker	ns	ns	F>E	—	(F>E)	ns
Paralichthys spp.	F>E	F>E	F>E	F>E	(F>E)	F>E
Photoperiod × depth						
Spot						
East/west D	B>S	B>S	B>S	—	(ns)	B>S
N	ns	S>B	S>B	—	(ns)	ns
Channel D	M B S	M B S	M B S	—	(B M S)	M B S
N	S M B	S M B	S M B	—	(ns)	S M B
Atlantic croaker						
East/west D	B>S	B>S	B>S	—	(ns)	B>S
N	B>S	ns	ns	—	(ns)	ns
Channel D	M B S	M B S	M B S	—	(ns)	M B S
N	M B S	ns	M S B	—	(ns)	ns
Paralichthys spp.						
East/west D	B>S	B>S	ns	ns	(ns)	B>S
N	ns	S>B	S>B	ns	(ns)	ns
Channel D	M B S	M B S	M B S	ns	(ns)	ns
N	M S B	S M B	ns	ns	(ns)	S M B
Tide × station[6]						
Spot						
Flood	E W C	E C W	E C W	—	[ns]	ns
Ebb	ns	W C E	ns	—	[ns]	W C E
Atlantic croaker						
Flood	E C W	E C W	E C W	—	[ns]	ns
Ebb	ns	C W E	C E W	—	[C W E]	W C E
Paralichthys spp.						
Flood	E C W	E C W	ns	ns	[ns]	ns
Ebb	ns	ns	ns	ns	[ns]	W E C
Tide × depth						
Spot						
East/west F	ns	ns	ns	—	[ns]	ns
Ebb	B>S	B>S	B>S	—	[ns]	B>S
Channel F	M S B	M S B	M S B	—	[ns]	M S B
Ebb	ns	B M S	B M S	—	[B M S]	B M S
Atlantic croaker						
East/west F	B>S	ns	ns	—	[ns]	B>S
Ebb	B>S	B>S	B>S	—	[ns]	B>S
Channel F	M B S	M S B	M S B	—	[ns]	M S B
Ebb	M B S	B M S	B M S	—	[ns]	M B S
Paralichthys spp.						
East/west F	ns	ns	ns	ns	[ns]	ns
Ebb	ns	ns	ns	ns	[ns]	ns
Channel F	M S B	M S B	ns	ns	[ns]	ns
Ebb	ns	ns	ns	ns	[ns]	ns

[1] [ ]—daytime data only from partial data set on 5 April; ( )—ebb tide data only from partial data set.
[2] Depths: surface (S), middepth (M), bottom (B).
[3] ns—no significant difference at $\alpha = 0.05$ level.
[4] Photoperiods: day (D), night (N).
[5] Tides: flood (F), ebb (E).
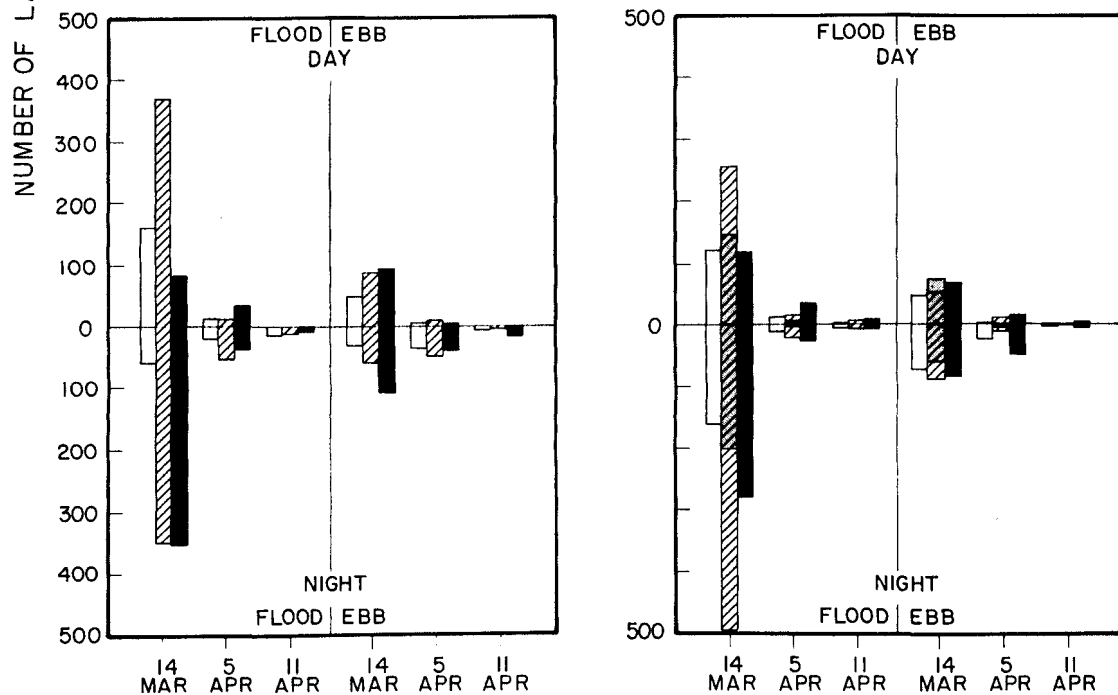[6] Stations: east (E), channel (C), west (W).

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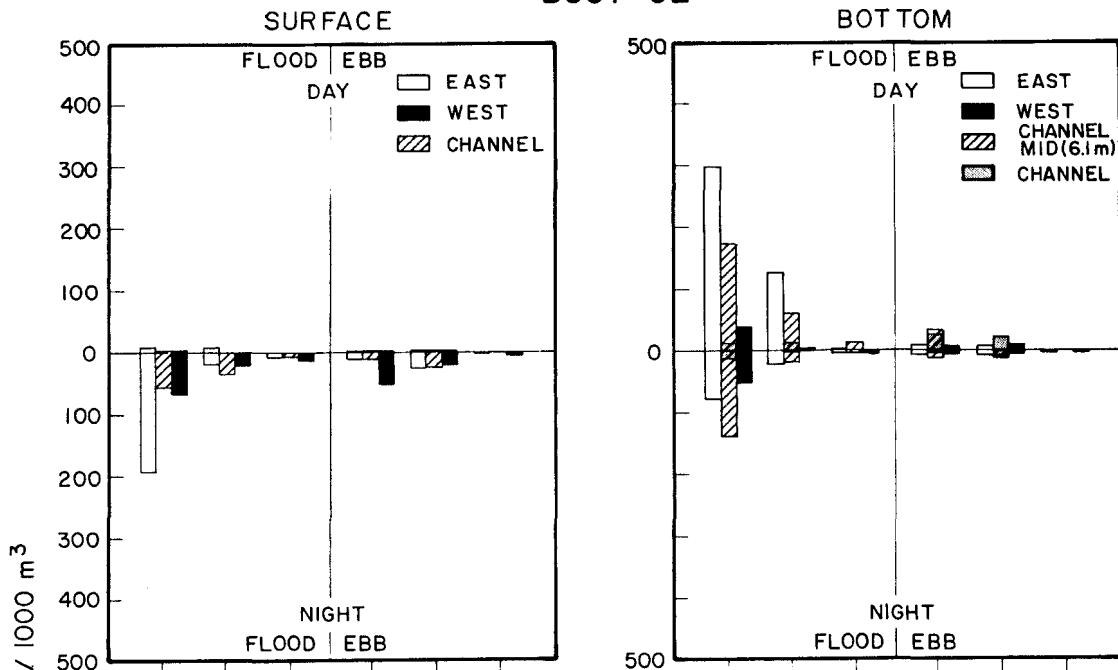
FIGURE 5.—Abundance of flounders (*Paralichthys* spp.) collected on three sampling dates at buoys 32 and 50. Data are stratified to shown mean values for each paired transect with respect to surface-bottom, day-night, and flood-ebb catches.

the largest mean catch. This pattern paralleled the flow of river water between tides; i.e., water tended to move upriver on the eastern shoal and returned on the west. If this phenomenon is real, it indicates the existence of a large-scale circulation pattern for postlarval populations.

The tide by depth interaction clearly described the immediate relationship of these organisms to tidal flows. Whereas the depth distribution of spot on flood tides was fairly uniform, bottom and mid-depth concentrations on ebb often exceeded those of surface values. Results were not quite as clear for Atlantic croaker because of their general bottom orientation; nevertheless, a tidal response was still evident for this species (Figure 4). Paradoxically, flounder showed little response to tide (compared with the main effect result), although a pattern similar to that of the other species is shown in the mean concentrations in Figure 5.

All of these comparisons are potentially influenced by diel activity, i.e., by downward migration during the day. Mean bottom values are influenced by this effect on both flood and ebb during daylight hours. One way of isolating the effect of photoperiod would be to examine the interaction of the three main effects (Table 3). Unfortunately, this interaction was rarely significant. Lack of significance may be a consequence of the use of a logarithmic scale in making

comparisons. Also, the power of tests on this three-way interaction is considerably less than that of tests of main effects and of two-way interactions. That diel migration was not entirely responsible for the observed patterns may be seen in the overall (24 h) differences between flood and ebb. Since two flood and ebb tides were sampled over each 24-h period, the effect of diel activity should be manifested on both tides; i.e., bottom orientation should occur on flood as well. Table 3 indicates that this was not the case. Furthermore, a perusal of the individual strata in Figures 3-5; e.g., an examination of surface night concentrations alone, shows that a clear tidal response was exhibited by all three species.

Length-Frequency Distributions

The possibility that buoy 50 was located within a primary nursery zone was alluded to earlier. This contention is also supported by length-frequency data which show that larger (older) fish tended to accumulate upriver near buoy 50. Unfortunately, larger fishes were probably not captured quantitatively since gear efficiency drops off rapidly after about 30 mm SL (Copeland et al. see footnote 8). Hence, only a qualitative picture of the age composition of a year class is possible. Nevertheless, distinct size differences occurred between buoys as indicated in Figures 6 and 7.
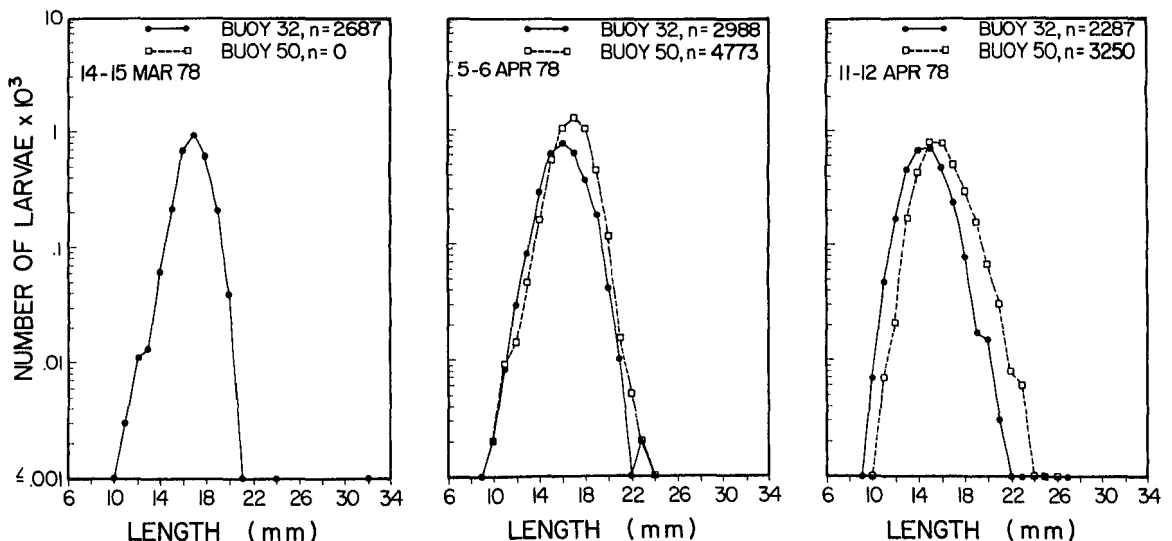

FIGURE 6.—Length-frequency distribution for spot, *Leiostomus xanthurus*, on the three collecting dates. This species was entirely absent from the vicinity of buoy 50 on 14-15 March.
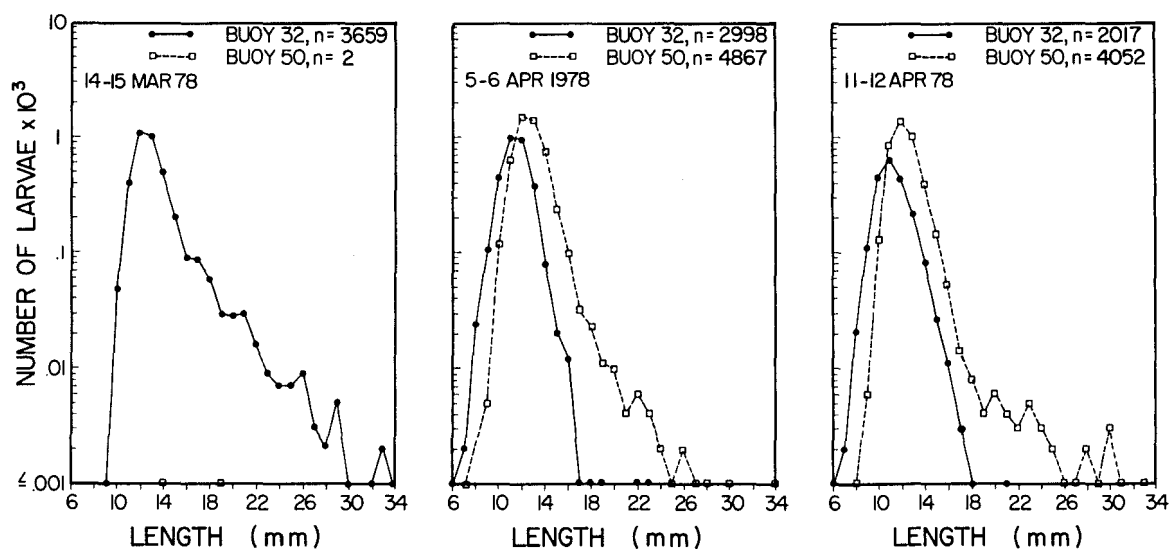
FIGURE 7.—Length-frequency distribution for Atlantic croaker, *Micropogonias undulatus*, on the three collecting dates. Only two individuals were captured in the vicinity of buoy 50 on 14-15 March.

Most interestingly, during the high-flow period on 14-15 March 1978, when spot and Atlantic croaker moved downriver, the larger fish accompanied the newer recruits to the vicinity of buoy 32. This is most evident in Figure 7 for Atlantic croaker. With the return of the salt front above buoy 50 in April, spot and Atlantic croaker returned upstream. For both species in this month, length-frequency distributions at buoys 32 and 50 were compared by Pearson chi-square tests. Significant differences ($P<0.05$) were found for all comparisons, with larger fish predominating upstream.

DISCUSSION

In contemplating the retention of bivalve larvae within the James River estuary, Wood and Hargis (1971) stated, "The point at issue is not whether such retention occurs, but whether evolved patterns of larval behaviour contribute significantly to the process." Evidence from the present investigation supports the premise that, by displaying specific behavioral responses, postlarvae of the three taxa studied were able to reach and stay within specific portions of the Cape Fear River estuary. This occurred despite intensive tidal flows and relatively high exchange ratios in the system.

Peak recruitment for winter-spawned larvae in the Cape Fear estuary and many other Atlantic coast estuaries occurs at a time when stratification and tidal exchange ratios are usually at a yearly maximum. The exchange ratio may exceed 0.70 in the Cape Fear estuary and flows above 1,700 m³/s have been recorded in January and February 1978 (Carpenter see footnote 4). Species recruited from the ocean also have the peculiar problem of initial entrance into the estuary and the avoidance of being washed out on the subsequent tide. By responding to a combination of hydrographic features of the estuary and perhaps to exogenous variables these species are able to avoid net seaward transport.

Active responses to light and diel migrations in the water column have been attributed to the larvae of barnacles (Fales 1928; Bassindale 1936; Bousfield 1955), oysters and other bivalves (Carriker 1951; Korringa 1952; Williams and Porter 1971: Wood and Hargis 1971), copepods (Schallek 1943), shrimp (Hughes 1969a, b, 1972; Williams and Deubler 1968), and fishes (Rogers 1940; Creutzberg 1961; Pacheco and Grant 1968; Lewis and Wilkens 1971; Graham 1972; Smith et al. 1978). However, differential avoidance of nets with respect to depth has also sometimes been suggested as the cause of diel "migrations" (e.g., Fore and Baxter 1972). Results of comparative studies using several kinds of collecting gear, including high-speed trawls (Thayer et al. in press), and the observed absence or low abundance of

most species (including those studied here) in daylight entrainment collections at a power plant located on the river near Southport (Copeland et al. see footnote 8) imply that this hypothesis is not tenable and support the contention that diel migrations actually do take place. If larvae were similarly stratified in the water column with respect to tide, a result paralleling that of the photoperiod response would be expected. By resting on the substratum during ebb, or at least by moving downward in the water column (below the level of no net motion), larvae would be transported in the landward direction.

Behavioral responses of spot, Atlantic croaker, and flounders to photoperiod and tide are summarized in Figure 8. Several important differences delineate ultimate habitat utilization by these species. Flounders apparently reacted to tidal flows by settling to the bottom, as has been suggested for oysters and shrimps (Carriker 1951; Hughes 1969a, b, 1972). When the lack of sig-

nificant tide by depth interaction and the presence of a tidal main effect are considered together, this hypothesis seems more tenable. To a degree, seeking boundary layers may be a general tidal response exhibited by all three species, making them difficult to sample on ebb (especially since the bottom nets were set 1 m above the substrate). The ability of flounders to effectively penetrate freshwaters also is enhanced by this behavior. Tidal flows above the salt boundary are substantial, certainly greater than the ability of flounder postlarvae to negotiate them directly. Saltatory movement upriver by "riding out" ebb on the bottom and responding to currents on flood would then be a primary mechanism for continued upstream migration.

Both spot and flounders were also observed to migrate toward the surface at night; significantly larger numbers of individuals were captured in this stratum both in midchannel and on the shoals, while Atlantic croaker tended to remain
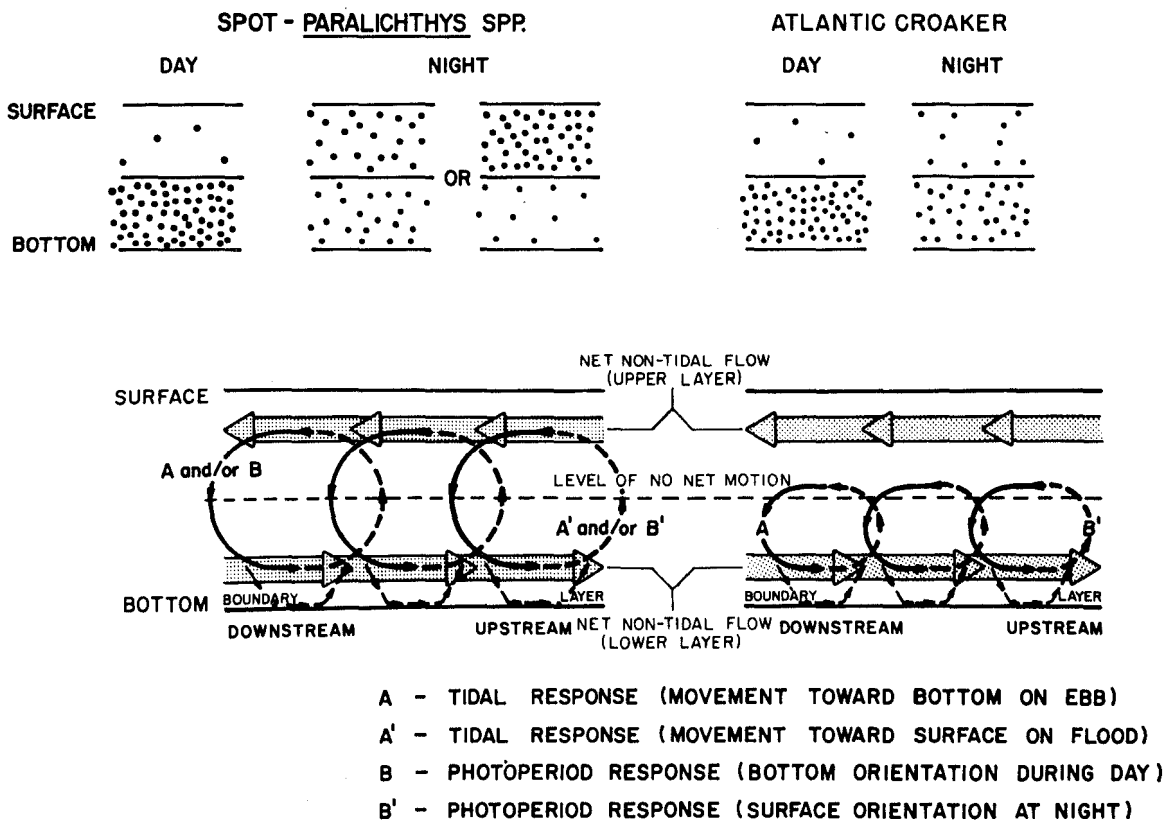

FIGURE 8.—Conceptual model for a larval retention mechanism based on response to photoperiod and tide. Details of the response differ for the three taxa (see text).

bottom oriented during this period. In studies of feeding by postlarval fishes in the Newport River estuary, N.C., Peters and Kjelson (1975) and Kjelson et al. (1975) demonstrated that spot were actively feeding only during the daytime and described them as carnivorous sight feeders. If the nighttime surface orientation observed for flounders and spot is not related to feeding activity, then to what might it be attributed?

We suggest that active migration into the marshes is aided by surface movement on flood tide at night. Since the mouths of many of these tidal creeks have sills, and since most are shallow and lack stratification, remaining near the bottom in the main stem would not aid postlarvae in lateral movements into the marshes. However, by staying near the surface on night flood tides, large numbers of individuals would be carried laterally into the marshes and other shoal areas, perhaps with the additional advantage of lower predation pressure.

Once in the marsh or other suitable shallow area, a tidal response elicited on ebb, i.e., a tendency to seek boundary layers near the bottom or toward the banks, would allow at least some members of the cohort carried into the system on flood to remain on ebb (Lewis and Mann 1971). This percentage need not be very high on each tidal cycle to produce a rapid population accumulation.

Species displaying a greater tendency to remain in the lower layers over 24 h should not be present in great numbers in shallow areas. This is precisely the case for Atlantic croaker. The marshes in the Cape Fear are not a major nursery zone for this species, as demonstrated by the nearly complete absence of postlarval Atlantic croaker from this habitat (Weinstein 1979). A noteworthy paradox arises when this species is considered over most of its geographic range. Atlantic croaker seem to prefer those estuaries with deep channels and are not taken in large numbers in the shallows (Welsh and Breder 1923; Wallace 1941; Suttkus 1955; Haven 1957; Nelson 1969; Chao and Musick 1977). It is suspected that in these estuaries, postlarval Atlantic croaker maintain their general bottom orientation and do not move laterally to any great extent; however, in several shallow estuaries along the Gulf of Mexico (Herke 1971; Parker 1971; Arnoldi et al. 1974; Yakupzack et al. 1977) young Atlantic croaker make extensive use of the marsh shallows. Thus, in those situations where deep channels are not predominant features of the system, Atlantic croaker will make use of the marsh shallows. This difference in distribution in the Gulf States might be further reconciled if temperature is taken into consideration. Temperature as a potential limiting factor for Atlantic croaker year class success in most middle Atlantic coast estuaries has been discussed by Joseph (1972). Remaining in the warmer waters of the deep channel during winter might enhance Atlantic croaker survival. The winters of 1976-77 and 1977-78 along the Atlantic coast have been colder than usual; greater utilization of shallow areas by Atlantic croaker might occur in warmer years.

Others also have observed that the river main stem at the head of the Cape Fear estuary is a primary nursery zone for Atlantic croaker and, to a more limited extent, for spot and flounders (Copeland et al. see footnote 8). In addition, the boundaries of this zone for certain species are dictated by freshwater flows and tend to shift with these flows. Although not captured quantitatively, larger spot and Atlantic croaker accumulated upriver in the vicinity of buoy 50 (Figures 6, 7). Although flounders were not measured, a similar result would be expected for these species.

In summary, we believe the data presented are consistent with the hypothesis that postlarvae exhibit behavioral patterns with respect to photoperiod and tide which are instrumental in enabling these organisms to: 1) accumulate in upstream nurseries by utilizing net nontidal flows in the lower layer, 2) make strong lateral movements into the marsh nurseries by migrating to the surface on flood tide at night, and 3) stay in both of these primary nurseries by dropping lower into or effectively out of the water column on ebb. The tidal response may be particularly important in well-mixed estuaries where upstream drift in the lower layers is negligible. In fact, it might be the primary mechanism employed by postlarvae to penetrate estuaries and reach suitable nursery habitats.

ACKNOWLEDGMENTS

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APPENDIX TABLE 1.—Three-way analysis of variance for spot, *Leiostomus xanthurus*, postlarvae captured at buoy 32, 14-15 March 1978. Catch data are $\log_{10}(10 + X)$ transformed.

Source	df	SS	MS	F	Source	df	SS	MS	F
Photoperiod, P	1	0.0551	0.0551	1.50	P × S	6	3.2729	0.5455	14.83*
Tide, T	1	0.2218	0.2218	6.03*	T × S	6	0.5744	0.9057	2.60*
Sites, S	6	2.6871	0.4479	12.17*	P × T × S	6	0.3805	0.0634	1.72
P × T	1	1.2493	1.2493	33.95*	Error	24	0.8831	0.0368	

Multiple comparisons (Numbers in parentheses are mean catch for each stratum.)
A. Tides
  Flood (100.7)>ebb (68.2)
B. Sites (Bonferroni *t*-tests; $\alpha = 0.05$)
  1. Depths: east and west
     Bottom (131.9)>surface (68.3)
  2. Depths: channel
     Largest: middepth(97.1) bottom (39.3) surface(39.2): smallest
  3. Stations
     Largest: east(109.5) west(90.6) channel(58.5): smallest

C. Photoperiod × tide (Bonferroni *t*-tests; $\alpha = 0.05$)
  Largest: flood/night(120.3) ebb/day(103.3) flood/day(81.1) ebb/night (27.2): smallest

D. Photoperiod × site (bonferroni *t*-tests; $\alpha = 0.05$)
  1. Photoperiod × depth: east and west
     Day: bottom(178.5)>surface(25.0)
     Night: ns[1]
  2. Photoperiod × depth: channel
     Day; largest: middepth(145.0) bottom(65.9) surface(8.8): smallest
     Night; largest: surface(79.5) middepth(49.2) bottom(3.9): smallest
  3. Photoperiod × station
     Day: ns
     Night; largest: west(97.8) east(91.1) channel(44.3): smallest

E. Tide × site (Bonferroni *t*-tests; $\alpha = 0.05$)
  1. Tide × depth: east and west
     Flood: ns
     Ebb: bottom(112.6)>surface(31.3)
  2. Tide × depth: channel
     Flood; largest: middepth(108.5) surface(58.1) bottom(9.3): smallest
     Ebb: ns
  3. Tide × station
     Flood; largest: east(158.6) west(110.1) channel(58.6): smallest
     Ebb: ns

*Significant at $\alpha = 0.05$.
[1]ns—no significant difference(s).

APPENDIX TABLE 2.—Three-way analysis of variance for Atlantic croaker, *Micropogonias undulatus*, postlarvae captured at buoy 32, 14-15 March 1978. Catch data are $\log_{10} (10 + X)$ transformed.

Source	df	SS	MS	F	Source	df	SS	MS	F
Photoperiod, P	1	0.0594	0.0594	1.46	P × S	6	2.1754	0.3626	8.91*
Tide, T	1	0.1086	0.1086	2.67	T × S	6	0.6195	0.1033	2.54*
Sites, S	6	9.3385	1.5564	38.24*	P × T × S	6	0.5752	0.0959	2.36
P × T	1	0.5152	0.5152	12.66*	Error	24	0.9769	0.0407	

Multiple comparisons (Numbers in parentheses are mean catch for each stratum.)

A. Photoperiod × tide (Bonferroni *t*-tests; α = 0.05)
   Largest: flood/night(301.4) ebb/day(249.7) flood/day(266.6) ebb/night(143.5): smallest

B. Sites (Bonferroni *t*-tests; α = 0.05)
   1. Depths: east and west
      Bottom (311.6)>surface (69.5)
   2. Depths: channel
      Largest: middepth(636.6) bottom(193.2) surface(28.1): smallest
   3. Stations: ns[1]

C. Photoperiod × site (Bonferroni *t*-tests; α = 0.05)
   1. Photoperiod × depth: east and west
      Day: bottom(404.6)>surface(25.7)
      Night: bottom(218.5)>surface(107.0)
   2. Photoperiod × depth: channel
      Day; largest: middepth(590.9) bottom(288.7) surface(6.3): smallest
      Night; largest: middepth(682.2) bottom(65.9) surface(57.2): smallest
   3. Photoperiod × station
      Day: ns
      Night: ns

D. Tide × site (Bonferroni *t*-tests; α = 0.05)
   1. Tide × depth: east and west
      Flood: bottom(336.3)>surface(110.7)
      Ebb: bottom(286.8)>surface(38.7)
   2. Tide × depth: channel
      Flood; largest: middepth(865.7) bottom(110.0) surface(31.6): smallest
      Ebb; largest: middepth(407.4) bottom(304.2) surface(23.6): smallest
   3. Tide × station
      Flood; largest: east(336.8) channel(335.8) west(110.1)
      Ebb: ns

*Significant at α = 0.05.
[1]ns—no significant difference(s).

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APPENDIX TABLE 3.—Three-way analysis of variance for *Paralichthys* spp. postlarvae captured at buoy 32, 14-15 March 1978. Catch data are $\log_{10} (10 + X)$ transformed.

Source	df	SS	MS	F	Source	df	SS	MS	F
Photoperiod, P	1	0.3217	0.3217	12.55*	P × S	6	1.7818	0.2970	11.58*
Tide, T	1	2.5208	2.5208	98.32*	T × S	6	1.1400	0.1900	7.41*
Sites, S	6	1.8388	0.3065	11.95*	P × T × S	6	0.4869	0.0812	3.17*
P × T	1	0.2309	0.2309	9.00*	Error	24	0.6154	0.0256	

Multiple comparisons (Numbers in parentheses are mean catch for each stratum.)

A. Photoperiod
    Night (50.3)>day (45.7)

B. Tide
    Flood(84.7)>ebb(11.1)

C. Sites (Bonferroni *t*-tests; $\alpha = 0.05$)
    1. Depths: east and west; bottom (62.3)>surface (37.8)
    2. Depths: channel
        Largest: middepth(89.8) surface(20.3) bottom(14.9): smallest
    3. Stations largest: east(79.3) channel(41.6) west(20.8): smallest

D. Photoperiod × tide (Bonferroni *t*-tests; $\alpha = 0.05$)
    Largest: flood/night(87.0) flood/day(82.3) ebb/night (10.5) ebb/day(11.6): smallest

E. Photoperiod × site (Bonferroni *t*-tests; $\alpha = 0.05$)
    1. Photoperiod × depth: east and west
        Day: bottom(89.0) >surface(3.4)
        Night: ns[1]
    2. Photoperiod × depth: channel
        Day; largest: middepth(103.4) bottom(19.1) surface(1.9): smallest
        Night; largest: middepth(76.1) surface(44.8) bottom(9.2): smallest
    3. Photoperiod × station
        Day: ns
        Night; ns

F. Tide × site (Bonferroni *t*-tests; $\alpha = 0.05$)
    1. Tide × depth: east and west
        Flood: ns
        Ebb: ns
    2. Tide × depth: channel
        Flood; largest: middepth(156.4) surface(29.4) bottom(12.4): smallest
        Ebb: ns
    3. Tide × station
        Flood; largest: east(160.3) channel(66.1) west(35.5): smallest
        Ebb: ns

*Significant at $\alpha = 0.05$.
[1]ns—no significant difference(s).