DENSITY AND DEPTH DISTRIBUTION OF LARVAL GULF MENHADEN, *BREVOORTIA PATRONUS*, ATLANTIC CROAKER, *MICROPOGONIAS UNDULATUS*, AND SPOT, *LEIOSTOMUS XANTHURUS*, IN THE NORTHERN GULF OF MEXICO

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ABSTRACT

Densities of larval gulf menhaden, *Brevoortia patronus;* Atlantic croaker, *Micropogonias undulatus;* and spot, *Leiostomus xanthurus*, compared among three transects in the northern Gulf of Mexico, indicated that all three species were more abundant at inshore (18 m isobath) than offshore stations (91 and 183 m isobaths). Gulf menhaden and Atlantic croaker were most abundant off Southwest Pass, Louisiana, a major outlet of the Mississippi River into the Gulf of Mexico. Gulf menhaden larvae caught at inshore stations were larger than those collected at offshore stations. Of the three species, only gulf menhaden showed any consistent pattern in vertical distribution. At inshore stations, gulf menhaden were concentrated near the surface at midday, but distributed across sampling depths (1 m, 6 m, and 12 m) at dawn, dusk, and midnight, a pattern opposite to that typically reported for larval fish. At offshore stations (with sampling depths of 1 m, 30 m, and 70 m), gulf menhaden larvae were present at 70 m, but most were caught near the surface. A concentration in surface waters was again most pronounced at midday.

Gulf menhaden, *Brevoortia patronus;* spot, *Leiostomus xanthurus;* and Atlantic croaker, *Micropogonias undulatus,* are thought to spawn offshore in winter months in the northern Gulf of Mexico (Nelson 1969; Fore 1970; Diaz 1982; Christmas et al. 1982). Larvae of the three species are transported inshore to nursery grounds in marshes and estuaries along the northern coast. One passive mechanism suggested for movement of gulf menhaden includes longshore advective transport, entrainment into the coastal boundary layer, and eventual transport into the estuary effected by the seasonal rise of sea level in spring (Shaw et al. 1985a). The passage of winter cold fronts can also be expected to influence transport.

Spawning of gulf menhaden occurs in shelf waters out to at least 91 m (Guillory et al. 1983), but is concentrated around the Mississippi River Delta (Fore 1970). Atlantic croaker apparently spawn in waters <54 m in depth (Diaz 1982), while spot spawn in waters >27 m (Dawson 1958; Nelson 1969). Gulf menhaden larvae spend 3 to 5 weeks at sea before entering estuaries when they are 12 to 25 mm in length (Reintjes 1970; Christmas and Etzold 1977; Guillory et al. 1983).

Fish larvae are nonrandom in their spatial distribution in both the vertical and horizontal dimensions. One primary influence on the vertical distribution of larvae is their diel vertical movement (migration) in the water column; larvae of many species rise to the surface by night and descend by day (e.g., Smith et al. 1978; Kendall and Naplin 1981; Sameoto 1982, 1984). Horizontal distribution is also dynamic, with dispersion and aggregation of larvae affected by such factors as adult spawning behavior, water mass movements, localized larval mortality, and larval behavior (Smith 1981; Houde 1982; Jahn and Lavenberg 1986).

In this study we examined the density and depth distribution of larval gulf menhaden, spot, and Atlantic croaker at three locations in the northern Gulf of Mexico, with emphasis on the area around Southwest Pass, LA, the main discharge of the Mississippi River among the delta distributaries. Size distributions of gulf menhaden were compared to determine if inshore larvae were older than offshore larvae, the expected pattern if adults are spawning primarily offshore and larvae are moving inshore.

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METHODS

Larvae were collected along three inshore-offshore transects (off Southwest Pass, LA; Cape San Blas, FL; and Galveston, TX) at stations positioned over the 18 m (10 fm), 91 m (50 fm), and 183 m (100 fm) isobaths (Fig. 1). Sampling took place on four cruises in December 1979, February 1980, December 1980, and February 1981. Collections were made with a Multiple Opening/Closing Net and Environmental Sensing System (MOCNESS, Wiebe et al. 1976). The MOCNESS consisted of nine 505 μm mesh Nitex[3] plankton nets with mouth openings of 1 m by 1.4 m. Due to equipment problems, only the inshore Southwest Pass station was sampled on the first cruise. Galveston stations were added to the sampling program on the February 1981 cruise.

MOCNESS nets were deployed in the following manner: Net 1 remained open as the MOCNESS descended from the surface to the deepest depth to be sampled. Nets 2 and 3 sampled at that depth, one at a time, and net 4 opened as the MOCNESS was raised to an intermediate depth, where nets 5 and 6 sampled. Net 7 was open while the MOCNESS was brought to the surface, where nets 8 and 9 fished. Discrete depth nets generally fished from 2 to 3 minutes before deployment of the next net. Sampling depths were approximately 12, 6, and 1 m at inshore stations and 70, 30, and 1 m at the offshore stations. At each station, MOCNESS casts were made at 0600, 1200, 1800, and 2400 h, with a towing speed of approximately 2 nmi/hour. Sensors on the MOCNESS provided continuous recording of temperature and depth. Two flowmeters, one mounted on top of the MOCNESS and one within the net opening, were used to calculate the volume of water sampled by each net and to detect net clogging. The mean volume filtered by each discrete depth net was 140 m^3 (SD = 101.2, n = 529).

The collection of one net at each discrete depth was preserved in 5% buffered formalin-seawater and the collection of the other was preserved in 70% ethanol. Formalin-preserved larvae were used in gut content analysis (Govoni et al. 1983), and alcohol-preserved larvae were used in otolith analysis of age and growth (Warlen in prep[4]). In the laboratory all fish larvae were removed from

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

[4]S. M. Warlen. Manuscr. in prep. Southeast Fisheries Center Beaufort Laboratory, National Marine Fisheries Service, NOAA, Beaufort, NC 28516.

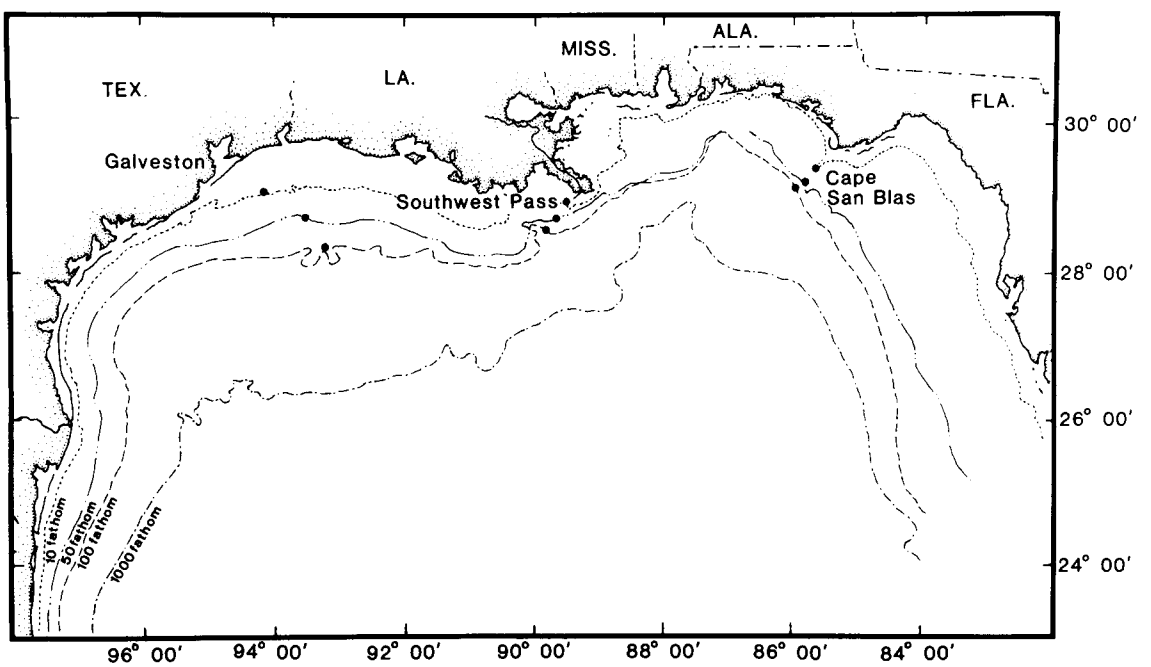

FIGURE 1.—Location of sampling transects and stations in the northern Gulf of Mexico.

the samples and counted. Gulf menhaden were measured (standard or notochord length) to the nearest 0.01 mm with an ocular micrometer. When more than 30 menhaden occurred in a sample, 30 individuals were randomly selected and measured (length measurements were not corrected for shrinkage). Due to the scarcity of larvae at outer stations, menhaden from both the 91 and 183 m Southwest Pass stations were combined in the comparison of offshore size distribution with inshore (restricted to the Southwest Pass station to allow valid comparison). Spot and Atlantic croaker were too rare at all offshore stations to allow size comparisons.

Analysis of vertical movement was based on the mean percentage of larvae caught at each of three discrete depths on each MOCNESS cast, allowing comparison among casts with widely varying densities of larvae. Gulf menhaden caught at the inshore stations were divided into three size classes to determine if vertical distribution varied with age. Because of the low number of larvae at the 183 m stations (see above), analysis of offshore vertical distribution was based on MOCNESS casts from both the 91 and 183 m stations. Mean densities at each depth were also calculated for each time of sampling.

RESULTS

Overall densities (number × 100 m^{-3}) of gulf menhaden, spot, Atlantic croaker, and the total of all species (these three species plus all others, including damaged and unidentifiable clupeids that may have been gulf menhaden) varied widely among cruises, stations, times, and depths. The majority of the 529 net tows did not catch any gulf menhaden (67%), spot (83%), or Atlantic croaker (82%). Smaller individuals of all three species, however, were probably not retained by the 505 μm mesh nets. In all but four cases, gulf menhaden were more abundant than spot or Atlantic croaker (Table 1). The density of all three species was generally greatest at the inshore (18 m) stations and declined offshore, with low or zero densities common at both offshore stations of Cape San Blas and Galveston (Table 1).

Gulf menhaden were most abundant at the Southwest Pass stations, except on the December 1980 cruise, when they were most abundant at the 18 m Cape San Blas station (Table 1). Atlantic croaker larvae were most abundant at the inshore Southwest Pass station in December 1980 and February 1981, but not in February 1980. Spot

TABLE 1.—Mean densities (SD in parentheses) of ichthyoplankton (larvae × 100 m^{-3}) collected at three stations at three sites in the northern Gulf of Mexico. Densities are averaged over three discrete depths and four times of day. Station 1 was over the 18 m isobath, station 2 over the 91 m isobath, and station 3 over the 183 m isobath. *n* = number of net tows. "Total larvae" includes the three target species and all others.

Cruise	Station	*n*	Total larvae	Gulf menhaden	Spot	Atlantic croaker
Dec. 1979	SW Pass 1	24	78.5 (88.9)	43.7 (66.9)	1.3 (2.3)	3.5 (3.9)
Feb. 1980	SW Pass 1	24	228.7 (281.4)	79.3 (122.5)	1.1 (0.3)	0.1 (0.3)
	SW Pass 2	23	32.1 (43.0)	7.4 (16.0)	0	0
	SW Pass 3	7	7.5 (5.9)	0.4 (0.7)	0	0
	San Blas 1	24	20.0 (14.4)	0.2 (10.5)	0.6 (0.9)	0.6 (0.8)
	San Blas 2	23	114.3 (85.3)	0.1 (0.2)	0.1 (0.3)	0.1 (0.4)
	San Blas 3	16	18.4 (13.2)	0	0	0
Dec. 1980	SW Pass 1	35	38.4 (30.4)	6.0 (8.0)	0.1 (0.2)	9.1 (15.2)
	SW Pass 2	24	56.0 (55.5)	8.8 (18.3)	0.2 (0.6)	3.1 (7.8)
	SW Pass 3	24	43.7 (38.4)	0.7 (2.1)	0	0
	San Blas 1	24	330.5 (618.6)	14.1 (42.4)	98.1 (259.3)	0.1 (0.1)
	San Blas 2	24	112.8 (83.2)	0	0.5 (1.2)	0.1 (0.3)
	San Blas 3	24	55.1 (61.0)	0	0	0
Feb. 1981	SW Pass 1	23	36.7 (49.7)	26.8 (43.8)	0.6 (0.9)	1.8 (2.6)
	SW Pass 2	22	65.8 (69.1)	13.6 (17.5)	0.6 (0.9)	0.6 (1.2)
	SW Pass 3	24	18.6 (15.0)	6.2 (11.8)	0.1 (0.1)	0
	San Blas 1	23	28.7 (15.8)	0	0	0
	San Blas 2	24	10.0 (9.0)	0	0	0
	San Blas 3	24	9.3 (6.8)	0	0	0
	Galveston 1	23	53.2 (26.1)	9.3 (6.8)	0	0
	Galveston 2	24	87.1 (65.0)	0.1 (0.1)	0	0
	Galveston 3	24	22.1 (16.4)	0	0	0

larvae were never very abundant except at the inshore San Blas station on the December 1980 cruise (Table 1), when a single dense patch of larvae was encountered on two successive MOCNESS casts (Govoni et al. 1985). Densities were as high as 993 larvae × 100 m^{-3}, an abundance not observed for other species and not approached by spot densities in any other sample. On the February 1981 cruise, no spot larvae were collected at this station. The occurrence of this aggregation, then, appeared to be a reflection of patchiness rather than geography.

TABLE 2.—Mean standard length (mm, SE in parentheses) of gulf menhaden caught on three cruises at inshore (18 m isobath) and combined offshore (91 and 183 m isobaths) stations off Southwest Pass, LA. *F* values are results of a two-way ANOVA comparing lengths among cruises and between stations.

	Station		*F*		
Cruise	Inshore	Offshore	Cruise	Station	Cruise × Station
Feb. 1980	15.2 (0.3)	8.9 (0.2)	21.8**	81.8**	62.6**
Dec. 1980	13.5 (0.3)	8.7 (0.3)			
Feb. 1981	12.3 (0.2)	12.3 (0.2)			

**$P < 0.001$.

An inshore-offshore comparison (Southwest Pass stations) of menhaden lengths revealed that on two of three cruises (February 1980 and December 1980) larvae were larger at the inshore station (Table 2). This was not the case on the third cruise, however, when mean lengths were similar. Results of a two-way ANOVA (Table 2) indicated significant differences in mean length for both main effects of station and cruise and for their interaction ($P < 0.001$). Thus, the pattern to the data is more complex than can be summarized by main effects alone. Length-frequency distributions indicated a bimodal pattern at the inshore station with most larvae in the larger size mode (Fig. 2). Larger larvae were not as common at the offshore stations except on the final cruise, when a bimodal pattern occurred offshore as well as inshore.

At the inshore stations, total larvae were generally distributed evenly among the three sampling depths at all times of day (Fig. 3), although

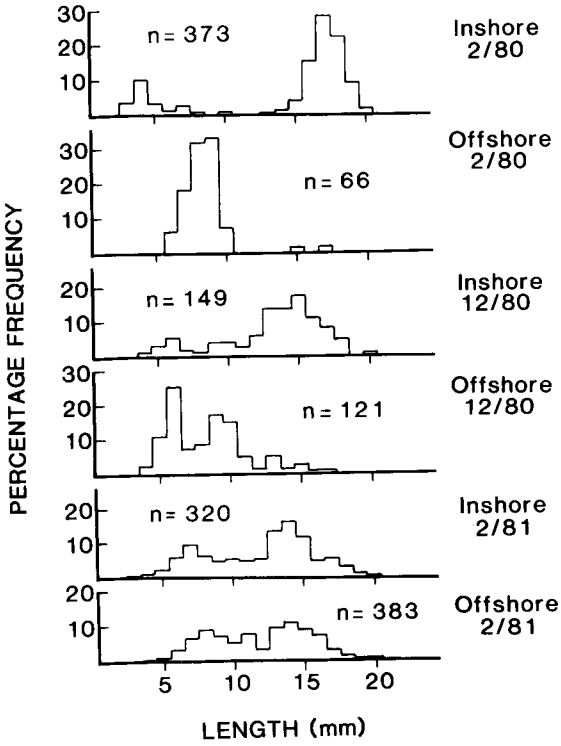

FIGURE 2.—Length-frequency distributions of gulf menhaden larvae collected from inshore (18 m isobath) and offshore (91 and 183 m isobaths combined) stations off Southwest Pass, Louisiana, on three cruises (February 1980, December 1980, and February 1981). n = number of larvae measured.

TABLE 3.—Mean density (larvae × 100 m^{-3}) at each discrete depth during each time period. MOCNESS casts in which no larvae of the target species were caught at any of the discrete depths were not included in calculation of means.

	Time			
Station/species	0600	1200	1800	2400
Inshore				
Total larvae				
1 m	68.23	120.97	341.10	76.36
6 m	56.01	25.76	144.20	86.82
12 m	42.44	25.24	69.20	173.78
Gulf menhaden				
1 m	31.72	37.35	48.83	12.44
6 m	4.54	0.14	101.06	22.74
12 m	13.16	0.60	29.93	22.37
Spot				
1 m	1.36	1.99	154.35	8.13
6 m	0.76	1.04	2.02	5.12
12 m	0.82	0.39	1.79	34.63
Atlantic croaker				
1 m	2.05	1.07	2.47	1.62
6 m	4.08	4.05	3.61	1.66
12 m	12.65	1.32	4.57	6.43
Offshore				
Total larvae				
1 m	103.90	57.37	57.64	49.65
30 m	35.41	21.30	63.37	42.37
70 m	23.38	8.35	14.93	14.29
Gulf menhaden				
1 m	23.70	35.60	14.36	14.19
30 m	7.47	0.00	7.77	3.76
70 m	0.22	0.39	0.42	0.29

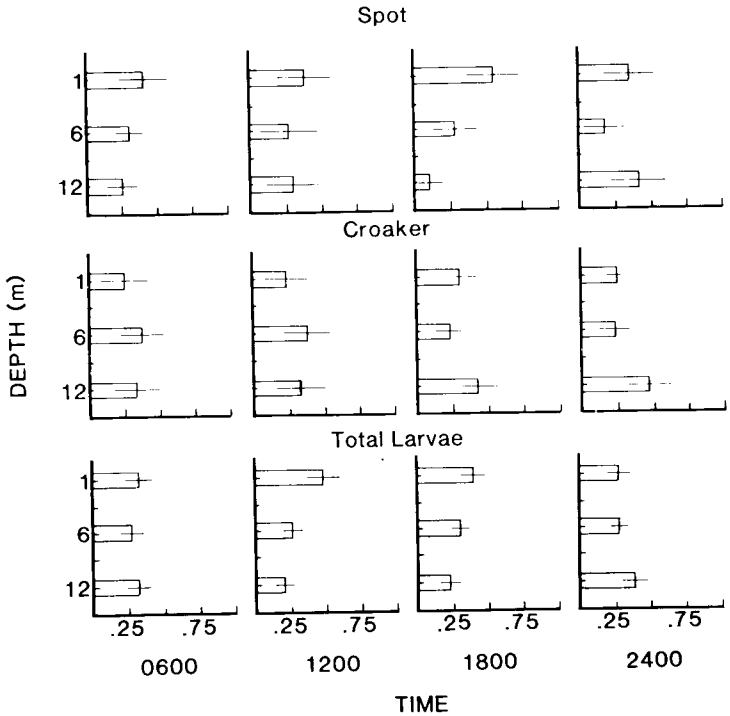

FIGURE 3.—Mean percentage of Atlantic croaker, spot, and total larvae collected at three discrete depths at inshore stations (18 m isobath). Error bars are standard errors.

mean densities were greater in surface waters at 1200 and 1800 h and in deeper waters at 2400 h (Table 3). The high mean densities of spot in surface waters at 1800 h and at 12 m at 2400 h (Table 3) were related to the encounter with the previously mentioned patch of larvae at Cape San Blas. When mean relative proportions were considered, however, these trends were moderated (Fig. 3). Although mean densities suggested a propensity for Atlantic croaker larvae to occur in deeper waters (Table 3), this trend also weakened when relative proportions were considered (Fig. 3). Gulf menhaden larvae in all three length groups were highly concentrated at the surface at 1200 h, but showed inconsistent patterns at other times (Fig. 4).

At the offshore stations (91 and 183 m), where there was a broader scale for vertical distribution, total larvae were generally less abundant at the deepest sampling depth (70 m, Table 3), but mean relative distributions indicated only slight trends (Fig. 5). Gulf menhaden larvae at offshore stations had greater densities at the surface at all times, with few larvae present at 70 m (Table 3). They again occurred almost exclusively in surface samples at 1200 h (Fig. 5). (Spot and Atlantic croaker were too rare at the offshore stations to allow examination of vertical distribution.)

Comparison of MOCNESS casts in thermally stratified versus isothermal water columns indicated that the presence of a weak thermocline did not inhibit vertical movement by any of the three target species or total fish larvae. Depth distributions were similar regardless of the thermal structure of the water. In most cases where a thermocline occurred, it was reversed, with colder water overlying warmer water, and a temperature difference of <5°C, the result of the Mississippi River plume.

DISCUSSION

High densities of gulf menhaden larvae at the Southwest Pass stations support the conclusions of Fore (1970) and Christmas and Waller (1975[5]) that spawning is concentrated around the Missis-

[5]Christmas, J. Y., and R. S. Waller. 1975. Location and time of menhaden spawning in the Gulf of Mexico. Unpubl. manuscr. Gulf Coast Laboratory, Ocean Springs, MS 39564.

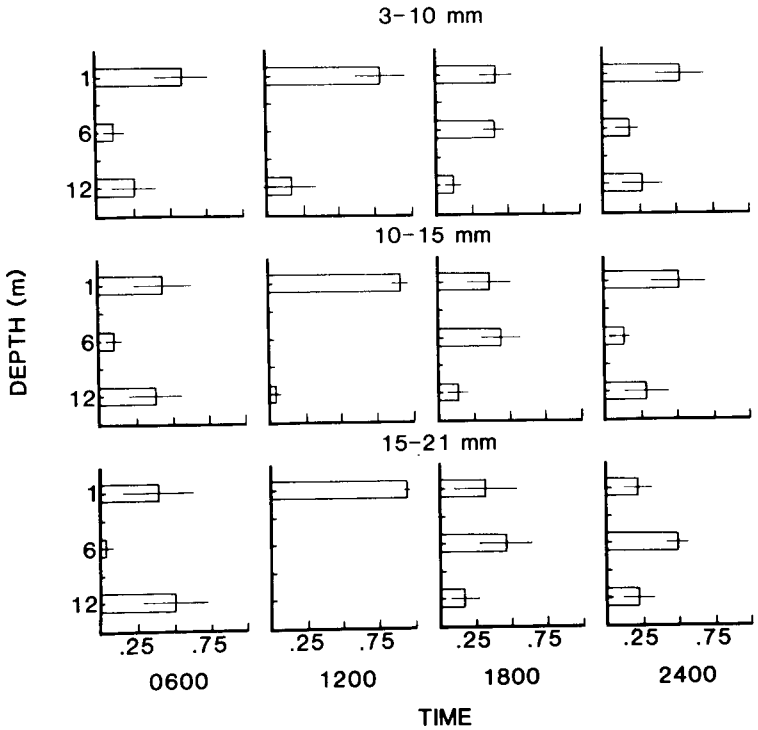

FIGURE 4.—Mean percentage of gulf menhaden larvae, divided into three size groups, collected at three discrete depths at inshore stations (18 m isobath). Error bars are standard errors.

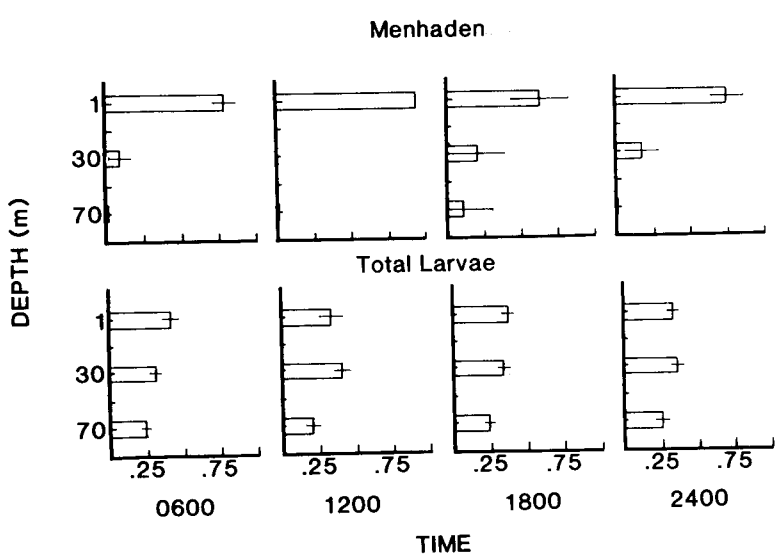

FIGURE 5.—Mean percentage of gulf menhaden and total larvae collected at three discrete depths at offshore stations (91 and 183 m isobaths). Error bars are standard errors.

sippi River Delta. In addition, Atlantic croaker larvae were rarely caught except at the inshore Southwest Pass station. High levels of nutrients (Riley 1937) and the resultant high plankton biomass in this region (Bogdanov et al. 1968) may make conditions exceptionally favorable for fish larvae.

Densities of all three target species showed a clear decline from inshore to offshore waters (Table 1). Shaw et al. (1985b) found a similar pattern for gulf menhaden larvae farther west along the Louisiana coast; densities were greatest in waters between the 14 and 24 m isobaths, with a shift in concentration to very nearshore waters by the end of the spawning season. The major spawning efforts of gulf menhaden, spot, and Atlantic croaker appear to occur in a relatively narrow band along the coast.

Size-frequency distributions of gulf menhaden larvae along the Southwest Pass transect showed that offshore stations were populated with smaller larvae on two of three cruises (Fig. 2, Table 2), but off western Louisiana, Shaw et al. (1985a) detected no difference in the size distribution of gulf menhaden from the 183 m isobath to inshore waters, except at stations immediately adjacent to shore (approximately 9 m in depth). Our observed pattern of decreasing size with distance from shore could arise either by adults spawning offshore and larvae growing as they move toward estuarine nursery grounds, or from serial spawning as adults move offshore during the protracted spawning season. The latter pattern is corroborated by Roithmayr and Waller (1963) and Fore (1970).

Only gulf menhaden showed clear evidence of a diel pattern in vertical distribution; they were concentrated almost exclusively at the surface at midday, but were more vertically dispersed at night at inshore stations. Size did not determine which larvae descended by dusk, because the vertical distribution was similar across all three size groups. In contrast, vertical migration of yellowtail flounder, *Limanda ferruginea*, and Atlantic herring, *Clupea harengus*, larvae varies with size, with smaller individuals remaining closer to the water surface (Smith et al. 1978; Wood 1971). Depth distributions of northern anchovy, *Engraulis mordax*, and white croaker, *Genyonemus lineatus*, also vary with age, with older larvae concentrating in deeper waters (Brewer and Kleppel 1986).

Gulf menhaden larvae >12 mm SL have deflated swimbladders by day and inflated swimbladders at night, achieved by swallowing air at the surface (Hoss and Phonlor 1984). This behavior, common among clupeoids (Hunter and Sanchez 1976; Uotani 1973), is thought to allow passive depth maintenance during nonfeeding hours at night (Hunter and Sanchez 1976). The observed depth distribution of gulf menhaden indicates that larvae must actively swim to stay at the surface during daylight hours. Apparently, the larvae slowly sink at night despite having gas in their swimbladders, and are, therefore, distributed at various depths. Data from offshore stations (Fig. 4) suggests, however, that most larvae are able to maintain their position within the upper 30 m of the water column.

The pattern of vertical distribution of gulf menhaden is opposite of that reported for numerous other species, in which larvae rise toward the surface at night and descend by day (e.g., Seliverstov 1974; Smith et al. 1978; Kendall and Naplin 1981; Sameoto 1982, 1984). A reversed pattern has also been observed for *Gadus macrocephalus* (Boehlert et al. 1985) and *Ammodytes personatus* (Yamashita et al. 1985). Yamashita et al. (1985) suggested that diurnal feeding requirements and nocturnal avoidance of upwardly migrating predators influence the vertical migration of *Ammodytes*. The behavior of Atlantic menhaden, *Brevoortia tyrannus*, is probably similar to gulf menhaden, as they are also reported to be more concentrated in surface waters by day than night (Thayer et al. 1983).

The presence of a weak thermocline with a gradient of <5°C did not appear to influence the vertical movement of fish larvae in this study. Other studies have reached conflicting conclusions. Ahlstrom (1959) and Loeb (1980) found thermal stratification with a temperature difference of 8° to 10°C very important in determining vertical distribution. Smith et al. (1978), Kendall and Naplin (1981), and Sameoto (1982), however, found that thermal gradients of 8° to 14°C did not inhibit vertical migration. The depth of the water column, the intensity of temperature change at the thermocline, and behavior of the species in question likely influence migration patterns. In relatively shallow water (Smith et al. 1978; Kendall and Naplin 1981; this study), thermal stratification appears less of a barrier than in deeper water. In this study larvae of gulf menhaden, spot, and Atlantic croaker largely remained within the upper 30 m, even when the water column was well-mixed to a depth of over 100 m. As we found for gulf menhaden, Brewer

and Kleppel (1986) noted significant diurnal depth stratification of larvae in the absence of thermal stratification. Absolute depths may be more important than thermal layers in determining vertical distribution when temperature differences are small.

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