Abstract.—The diel pattern in vertical distribution of red drum *Sciaenops ocellatus* larvae was described from plankton collections taken at three depths and three time periods over a 24-hour period during five cruises in inner shelf waters of the northcentral Gulf of Mexico (east Louisiana–Mississippi–Alabama region). Larvae ranging in mean size from 1.7 to 5.0 mm were vertically stratified at both offshore and nearshore locations over bottom depths <25 m. Diel periodicity in vertical stratification was evident in four cruises, with larvae being concentrated higher in the water column during daylight hours than at night. There was no clear relationship between vertical aggregation of red drum larvae and temperature or salinity profiles or prey microzooplankton distribution.

Diel Vertical Distribution of Red Drum *Sciaenops ocellatus* Larvae in the Northcentral Gulf of Mexico

Joanne Lyczkowski-Shultz
John P. Steen Jr.
Gulf Coast Research Laboratory
P.O. Box 7000, Ocean Springs, Mississippi 39564

Diel vertical migration has been observed among the larvae of many taxa of marine fishes in diverse environments ranging from estuaries to the open sea (see Neilson and Perry 1990 for recent review), and under both stratified and well-mixed hydrographic conditions (Ahlstrom 1959, Smith et al. 1978, Kendall and Naplin 1981, Brewer and Kleppel 1986, Perry and Neilson 1988). The most frequently observed pattern of larval movement has been daytime concentration at lower depths with subsequent movement towards the surface at night (Smith et al. 1978, Kendall and Naplin 1981, Boehlert et al. 1985), but the reverse tendency has also been noted (Hempel and Weikert 1972, Boehlert et al. 1985, Yamashita et al. 1985, Sogard et al. 1987, Neilson and Perry 1990). Another pattern is one where larvae are aggregated at depth during daytime but become more dispersed at night (Brewer and Kleppel 1986, Heath et al. 1988). Ontogenetic differences in vertical distribution and migration patterns have frequently been observed (Brewer and Kleppel 1986, Castonguay and McCleave 1987, Stephenson and Power 1988). The adaptive significance of vertical migration remains unknown (Pearre 1979), but some inferred or proposed advantages to fish larvae include maintenance of position relative to prey (Hunter and Sanchez 1976); predator avoidance (Zaret and Suffern 1976); energy conservation through swimbladder inflation at the surface (Hunter and Sanchez 1976); maximization of energy intake through depth-mediated thermoregulation (Wurtsbaugh and Neverman 1988); and enhancement of transport to nursery grounds (Miller et al. 1984, Norcross and Shaw 1984, Boehlert and Mundy 1988). Knowledge of vertical distribution patterns among early life stages is necessary, not only to better understand early ecology but also to improve the design of broadscale surveys for resource and population assessments using the abundance of fish eggs and larvae (Ahlstrom 1959, Stephenson and Power 1988, Perry and Neilson 1988).

Data presented here on diel changes in vertical distribution of red drum *Sciaenops ocellatus* larvae came from an ongoing, comprehensive investigation begun in 1983 into the early ecology (Lyczkowski-Shultz et al. 1988), age and growth (Comyns et al. 1989), and spawning seasonality and biomass (Comyns et al. 1991) of this commercially and recreationally valuable sciaenid in coastal and shelf waters of the northern Gulf of Mexico.

Materials and methods

Ichthyoplankton collections were taken during five, 24-hour cruises in September and October 1984 and 1985 in the general area east of the Mississippi River delta and south of the Mississippi barrier islands over the east Louisiana–Mississippi–Alabama shelf (Fig. 1). Discrete-depth

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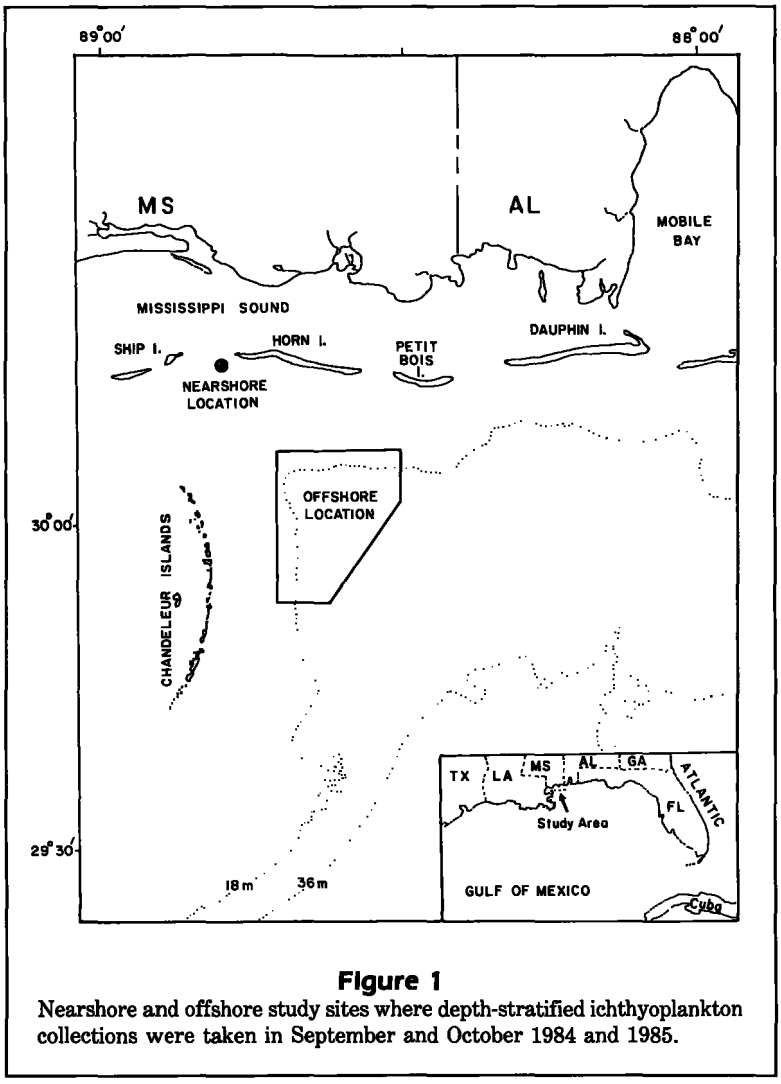

Figure 1
Nearshore and offshore study sites where depth-stratified ichthyoplankton collections were taken in September and October 1984 and 1985.

samples were taken offshore in the vicinity of a "windowshade," subsurface (5m) current drogue as it was tracked from the ship throughout the duration of a cruise in an attempt to repeatedly sample the same patch of fish larvae and zooplankton (Lyczkowski-Shultz et al. 1988). The drogue traveled, on average, 13km during a sampling period, typically at varying compass headings over water depths of 18–25m. During each cruise, collections were usually made during early to late afternoon of the first day, then in the middle of the night (usually prior to midnight), and in the morning (after sunrise) of the second day. In all but one instance, dawn and dusk periods were specifically avoided. Times of sunrise and sunset on sampling dates in September and October 1984 and 1985 ranged from 0543 to 0600 hours, and from 1733 to 1819 hours central standard time (CST), respectively. During three of the five cruises, additional samples were taken at a fixed, shallow water station (12m) located 15–19km NNW of the offshore sampling area during midday hours of the second day (nearshore, Fig. 1). Times of high and low tide were determined using predictions for tide stations nearest the offshore sampling sites (NOAA-NOS Tide Tables).

Sampling gear consisted of a 1×1.4m, multiple-net Tucker trawl with an effective mouth opening of 1m² when fished at a 45° angle, and a double-release mechanism operated manually with messengers. Mean tow speeds varied from 1.5 to 2.5 knots (0.8–1.3m/s). At the offshore location, three Tucker trawl casts were made during each time period. A cast consisted of all three 333-μ mesh nets being fished in horizontal 5-min hauls at one nominal depth level at a time. These sampling depths were 1, 5, and, most typically, 11 or 12m. At the nearshore location, each of the three nets were fished at 1, 3, and 7 or 9m, but the nets were of different mesh sizes: 333, 505, and 760μ. Offshore catch data from the three net samples at each depth were pooled for analyses for cruises 84-9-1, 84-10-1, and 85-9-1, even though only net 2 was both opened and closed at depth. Contamination in nets 1 and 3 was considered to be minimal due to the relatively short time for their deployment and retrieval, less than 30 seconds in total. Comparison of catches from the three nets indicated that contamination had not seriously affected our results, as there was little to no overlap among adjacent sampling depths in the range of observed densities (as measured by each of the three nets) per sampling period (Fig. 2). Catch data from all three nets of different mesh sizes at the nearshore site were combined since sampling effort, i.e., number of samples per mesh size at each depth, was the same. Due to time constraints, only net 2 samples (the 333-μ mesh net at the nearshore site) were sorted from cruises 84-9-2 and 85-10.

Fishing depth was monitored throughout each tow via the depth sensor of an electronic conductivity/temperature/depth probe package (CTD) which was mounted 0.5m above the trawl frame on the conducting/towing cable. Except for the nearsurface or 1m depth stratum, actual sampling depths exceeded nominal depths by 0.5m. Target or nominal sampling depths were maintained throughout each tow by adjusting the amount of wire out.

Flowmeters in each net measured volume filtered which generally ranged between 200 and 300 m³.

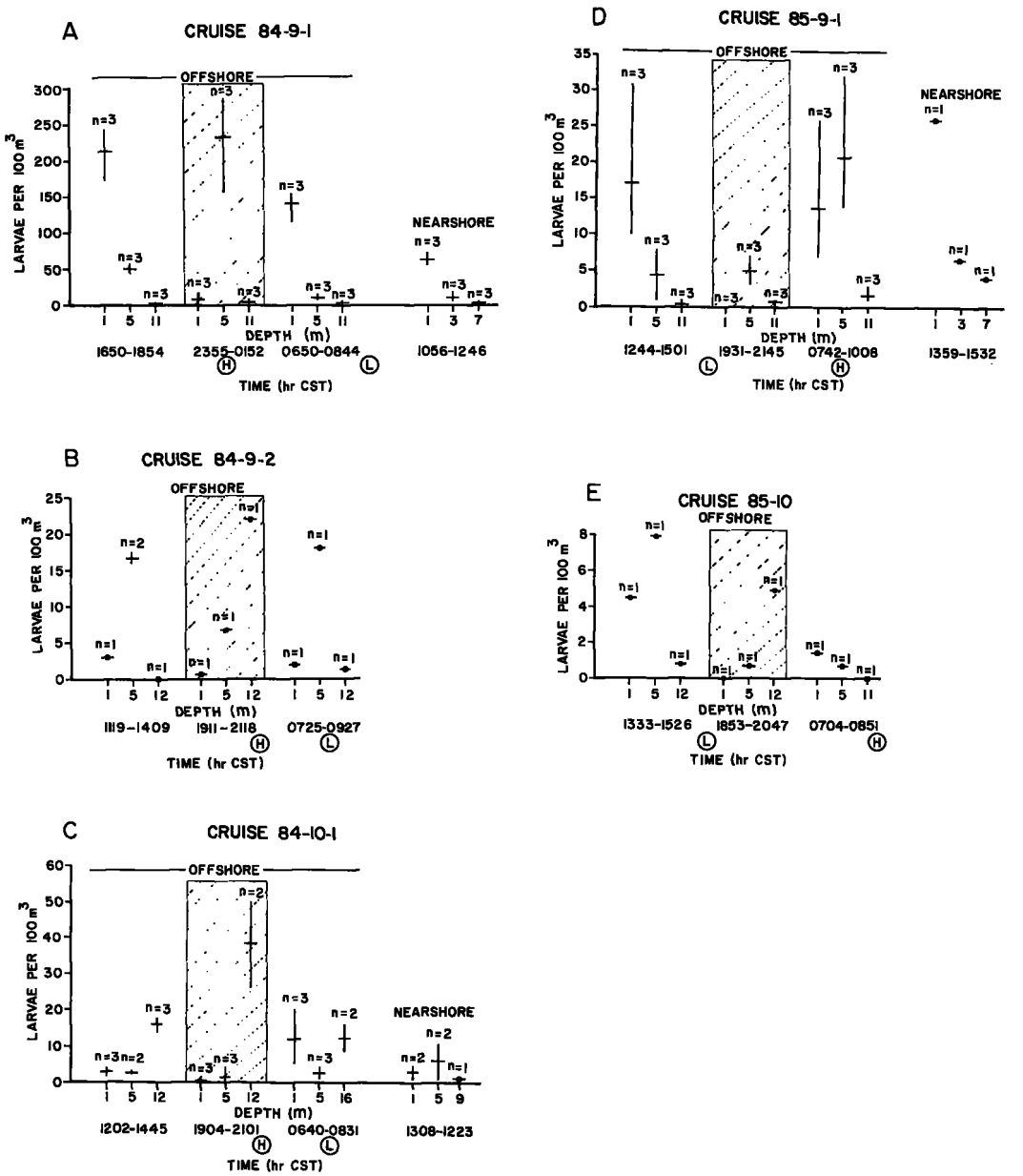

Figure 2

Mean and range in density of red drum larvae *Sciaenops ocellatus* by sampling depth and time at offshore and nearshore sites during cruises in 1984 and 1985. n = number of collections per sampling period. Crosshatching denotes nighttime observations. Encircled H and L symbols mark the approximate times of high and low tide.

Vertical profiles of temperature and salinity prior to sample collection were obtained with the CTD.

Ichthyoplankton samples were preserved at sea in 5–10% formalin and were later (1 week to 6 months) transferred to 70% ethanol for final preservation. In the laboratory, all larvae were removed from either the entire sample or from a one-half aliquot which was obtained using a Motoda plankton splitter (Van Guelpen et al. 1982). Standard length (SL) of larvae was measured to the nearest 0.1mm at 12× using a stereomicroscope. Larval densities are reported as number per 100 m^3.

Zooplankton samples were collected by pumping water up from the same depths as ichthyoplankton

collections with a 38L/min capacity diaphram pump and filtering approximately 0.3–0.5m³ through nested 63 and 25μ mesh nets on deck. Zooplankton samples were preserved in 5% formalin. The average time between collection of fish larvae and zooplankton was 2.5 hours, with values ranging between 21 minutes and 4 hours.

Statistical analysis of diel vertical patterns in larval red drum abundance was conducted using nonstandard, chi-squared, goodness-of-fit procedures (McCleave et al. 1987). First, the standardized residual of larval density at each depth was calculated,

$$SR_i = \frac{(N_i - E_i)}{\sqrt{E_i}}$$

where N_i = observed catch at depth i, and E_i = expected catch at depth i. E_i was calculated by multiplying the total number of red drum larvae caught during a time period (all depths combined) by the proportion of total fishing effort at that depth, i.e., the volume filtered at that depth divided by the total volume filtered during the time period. The sum of squared SR_i's yields the chi-squared (χ^2) statistic for testing the null hypothesis that within a single time period the density of red drum larvae is uniform with depth. A second null hypothesis—that the vertical distribution of larvae remains unchanged over the diel cycle, i.e., among the three sampling periods—was investigated using the chi-squared test for heterogeneity (a nonstandard, goodness-of-fit test; Sokal and Rohlf 1981). This was accomplished by subtracting the χ^2 value for the combined data set (three time periods) from the sum of the individual χ^2's for each time period.

Results

Depth-stratified ichthyoplankton collections during afternoon, night, and morning, over a 24-hour period during five cruises, were examined for patterns in vertical distribution of red drum larvae. Larvae were vertically stratified in both offshore and nearshore waters (Fig. 2). Larvae were usually more abundant at 1 and/or 5m than at 11, 12, or 16m at the offshore location, and than at 7 or 9m at the nearshore location. In two of the three cruises in which both offshore and nearshore sites were sampled, the depth of greatest abundance (at a comparable time period) was the same at both nearshore and offshore sites (Fig. 2A, D).

Vertical stratification at the offshore location appeared to have a diel component in four cruises (Fig. 2A, B, D, E). The most consistent diel pattern was a decrease in abundance, relative to afternoon values, at 1m and a relative increase at 5 or 11–12m during nighttime hours. The following morning, abundance at 1 and/or 5m was higher than the nighttime values at those depths. During cruise 84-9-2 the diel shift in maximum abundance occurred between 5 and 12m, with abundance at 1m remaining relatively constant throughout the 24-hour period (Fig. 2B). Mean density of larvae during cruise 84-10-1 was highest at 12m during both afternoon and night, but in the morning maximum density values were observed at both 1 and 16m (Fig. 2C).

The most distinct pattern of vertical stratification was observed in cruise 84-9-1 where the center of abundance of red drum larvae shifted from 1 to 5m and back to 1m over the three time periods, with no overlap in mean density or range in densities among adjacent depths within a sampling period (Fig. 2A). Mean density at 1m in the afternoon was remarkably similar to the mean density at 5m at night, 214.5 vs. 234.5, but by morning of the next day maximum abundance had declined to 141.0. Although vertical stratification was evident in the other three offshore data sets, the diel pattern was less distinct.

Nonstandard, chi-squared goodness-of-fit analyses were used to test two null hypotheses (McCleave et al. 1987): that (1) red drum larvae were homogeneously distributed over the three sampling depths, and (2) the vertical distribution of larvae remained unchanged over three sampling times spanning a diel cycle. In 17 of 18 cases, including both offshore and nearshore sites, null hypothesis 1 was rejected at the 0.01 significance level (Tables 1 and 2). In all five data sets from the offshore site, null hypothesis 2 was also rejected at the 0.01 significance level, i.e., larval depth distribution did not remain the same among the sampling periods (Table 1).

The sign and magnitude of standardized residual deviations, SR_i values, were examined to determine the diel pattern in vertical distribution of red drum larvae (Table 1). In four of five cruises, the depth of greatest larval abundance was higher in the water column during afternoon hours than at night (Fig. 2). In two cruises (84-9-1 and 84-9-2), the depth of greatest larval abundance on the following morning was the same as on the preceding afternoon and, therefore, higher in the water column than on the preceding night. In one cruise (85-9-1), although the depth of greatest abundance (5m) in the morning was the same as at night, abundance at 1m (depth of greatest abundance during the preceding afternoon) had increased relative to the nighttime value. The morning sampling period of cruise 85-10 was the only case where larvae were homogeneously distributed throughout the water column. During the only cruise (84-10-1) in which depth of greatest larval abundance was the same in afternoon

Table 1

Analyses of the null hypotheses: (1) red drum larvae are homogeneously distributed over three sampling depths, and (2) the vertical distribution of larvae is similar over three sampling times spanning a diel cycle. Data from five cruises from offshore Mississippi waters in September and October, 1984 and 1985. N_i = number of larvae at depth i; E_i = expected number of larvae at depth i; SR_i = standardized residual deviation of observed from expected catch at depth i.

	Afternoon (1650–1854 hrs)				Night (2355–0152 hrs)				Morning (0650–0844 hrs)				Times combined		
Depth	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 84-9-1, 13–14 September 1984															
1	835	1807	757	+38	647	63	587	−22	722	993	336	+36	2863	1680	+29
5	610	308	553	−0	916	2217	830	+48	741	84	345	−14	2609	1728	+21
11	896	8	812	−28	1011	53	917	−28	938	41	437	−19	102	2166	−44
Total	2341	2123			2575	2333			2401	1118					
Chi-square χ^2				2360**				3600**				1841**			3248
$\chi^2_{0.01,\ 2df} = 9.21$															
$\chi^2_{het} = \chi^2_{aft} + \chi^2_{night} + \chi^2_{morn} - \chi^2_{comb} = 7801 - 3248 = 4553^{**}$															
$\chi^2_{0.01,\ 4df} = 13.28$															
	Afternoon (1119–1409 hrs)				Night (1911–2118 hrs)				Morning (0725–0927 hrs)				Times combined		
Depth	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 84-9-2, 26–27 September 1984															
1	415	12	33	−0.4	382	2	36	−6	209	4	17	−3	18	85	−7
5	432	72	34	+6	387	26	36	−2	332	60	27	+6	158	97	+6
11	208	0	17	−4	346	76	32	+8	307	4	25	−4	80	73	+0.8
Total	1055	84			1114	104			847	68					
χ^2				58**				94**				69**			92
$\chi^2_{het} = 220 - 92 = 128^{**}$															
	Afternoon (1202–1445 hrs)				Night (1904–2101 hrs)				Morning (0640–0831 hrs)				Times combined		
	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 84-10-1, 10–11 October 1984															
1	986	30	73	−5	741	2	113	−10	700	83	61	+3	115	221	−7
5	978	28	72	−5	752	10	115	−10	769	19	67	−6	57	228	−11
12(16)	998	160	73	+10	833	344	128	+19	982	112	86	+3	616	287	+19
Total	2962	218			2325	356			2451	214					
χ^2				154**				573**				50**			557
$\chi^2_{het} = 777 - 557 = 220^{**}$															
	Afternoon (1244–1501 hrs)				Night (1931–2145 hrs)				Morning (0742–1008 hrs)				Times combined		
	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 85-9-1, 11–12 September 1985															
1	721	131	47	+12	666	0	13	−4	677	92	70	+3	223	130	+8
5	779	36	51	−2	652	34	13	+6	636	130	66	+8	200	130	+6
11	1103	2	72	−8	667	6	13	−2	984	16	102	−9	24	187	−12
Total	2603	169			1985	40			2297	238					
χ^2				223**				51**				142**			246
$\chi^2_{het} = 416 - 246 = 170^{**}$															
	Afternoon (1333–1526 hrs)				Night (1853–2047 hrs)				Morning (0704–0851 hrs)				Times combined		
	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	Volume	N_i	E_i	SR_i	N_i	E_i	SR_i
Cruise 85-10, 10–11 October 1985															
1	224	10	10	+<0.1	305	0	6	−2	286	4	2	+1	14	18	−0.9
5	254	20	11	+3	285	2	5	−1	286	2	2	−<0.1	24	19	+1
12(11)	240	2	11	−3	284	14	5	+4	281	0	2	−1	16	18	−0.5
Total	718	32			874	16			853	6					
χ^2				14**				22**				4ns			3
$\chi^2_{het} = 400 - 3 = 37^{**}$															

Table 2

Analyses of the null hypothesis: red drum larvae are homogeneously distributed over three sampling depths at the nearshore site. N_i = number of larvae at depth i; E_i = expected number of larvae at depth i; SR_i = standardized residual deviation of observed from expected catch at depth i.

Cruise 84-9-1					Cruise 84-10-1					Cruise 85-9-1				
Depth	Volume	N_i	E_i	SR_i	Depth	Volume	N_i	E_i	SR_i	Depth	Volume	N_i	E_i	SR_i
1	757	469	169	+23	1	706	20	35	−3	1	591	84	53	+4
3	847	94	189	−7	5	1025	81	51	+4	3	275	18	25	−1
7	1025	25	229	−13	9	393	4	19	−4	7	498	20	45	−4
Total	2629	588				2124	105				1364	122		
χ^2				761**					37**					34**
$\chi^2_{0.01,\,2df}$ = 9.21														

and night sampling periods, there was an increase in abundance at 1 m in the morning hours with mean densities at 1 and 16 m being identical.

Size composition of red drum larvae within cruises remained relatively constant except during cruise 85-9-1 when mean size in the morning was much smaller than during two previous sampling periods (Table 3). Red drum larvae did not appear to be depth-stratified by size.

Vertical profiles of temperature and salinity taken just prior to sampling during each of the five cruises consistently showed the water column to be well-mixed (Fig. 3). There was no evidence of a well-defined or persistent thermocline to which red drum larvae might orient. Mean temperature averaged over sampling depths was 3°C higher during cruises 84-9-1&2 and 85-9-1 than during cruises 84-10-1 and 85-10. Salinity varied somewhat more throughout the water column than did temperature but usually differed no more than 2–3 ppt between September and October observations. Isohaline conditions generally prevailed within the upper 12 m of the water column during all cruises except 84-9-1, when a difference in salinity of 5 ppt between the surface and 12 m was observed throughout all three sampling periods (Fig. 3A). Yet the same general pattern in vertical stratification of red drum larvae was evident within that salinity gradient as was observed under more isohaline conditions. There was also no consistent relationship between tidal stage and vertical position of larvae (Fig. 2). This was especially evident during cruises 84-9-1 and 85-9-1 when red drum larvae showed the same general pattern in vertical distribution under the opposite stage of the tide.

Moonlight intensity as influenced by moon phase, time of moonrise, and presence/absence of cloud cover did not appear to explain similarities or differences among cruises in nighttime vertical distribution of red drum larvae. Cruises 84-9-2, 85-9-1, and 85-10 were all conducted within 2 to 3 days of the new moon, i.e., when moonlight was at a minimum. Cruises 84-9-1 and 84-10-1 were both conducted 2 to 3 days after the full moon, on cloudless nights with moonrise occurring early in the evening, i.e., when moonlight was near maximum.

The vertical distribution of prey microzooplankton, based on a single collection per depth, was compared with the depth of maximum abundance of red drum larvae at the offshore location (Table 4). Microzooplankton were grouped into three categories based on examination of larval gut contents, net-caught zooplankton, and statistical comparisons of diet and prey availability

Table 3

Mean standard length in millimeters (standard error of the mean in parenthesis) of red drum larvae at three sampling depths and time periods (afternoon, night, and morning) during five cruises in offshore waters.

Depth	Afternoon	Night	Morning
	Cruise 84-9-1		
1	2.8 (0.02)	2.7 (0.03)	2.9 (0.02)
5	2.7 (0.02)	2.7 (0.02)	2.6 (0.05)
11	2.8 (0.12)	2.7 (0.05)	2.6 (0.06)
	Cruise 84-9-2		
1	2.9 (0.13)	1.8 (—)	2.3 (0.48)
5	2.5 (0.04)	2.9 (0.04)	2.7 (0.08)
12	—	2.9 (0.05)	2.6 (0.68)
	Cruise 84-10-1		
1	4.7 (0.31)	3.8 (—)	4.4 (0.15)
5	4.0 (0.24)	4.6 (0.27)	4.3 (0.29)
12 (16)	3.9 (0.11)	4.5 (0.11)	4.0 (0.09)
	Cruise 85-9-1		
1	4.7 (0.05)	—	1.9 (0.13)
5	4.4 (0.11)	4.6 (0.20)	2.1 (0.14)
11	4.6 (—)	5.0 (0.31)	1.7 (0.02)
	Cruise 85-10		
1	3.7 (0.15)	—	3.3 (0.16)
5	3.4 (0.11)	4.6 (—)	4.4 (—)
12 (11)	1.3 (—)	3.6 (0.11)	—

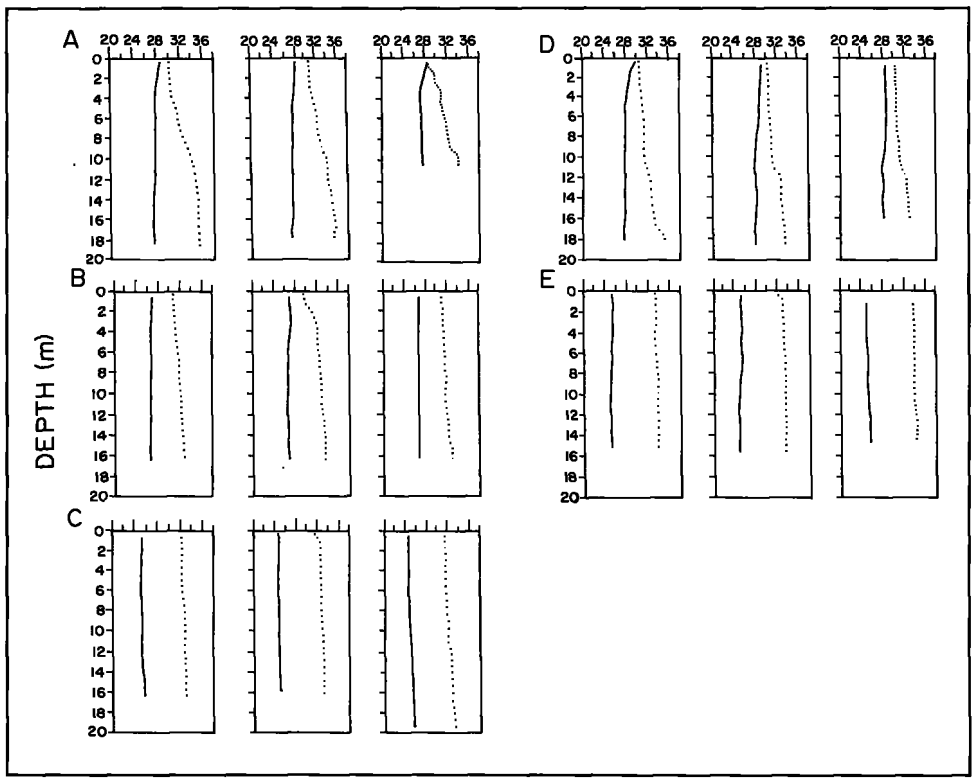

Figure 3
Vertical profiles of temperature (°C, solid line in each plot) and salinity (ppt, dotted line in each plot) during afternoon (left plot), night (center plot), and morning (right plot) sampling periods from cruises: (A) 84-9-1, (B) 84-9-2, (C) 84-10-1, (D) 85-9-1, (E) 85-10.

Table 4
Density of prey microzooplankton (n/L) at three sampling depths and time periods (afternoon, night, and morning) during five cruises in offshore waters. Asterisks indicate depth of highest observed red drum density for that time period. A = density of "preferred" prey; B = density of crustacean nauplii; C = density of total prey zooplankton in the size range 63–230 μ maximum width (excluding appendages).

	Afternoon			Night			Morning		
Depth	A	B	C	A	B	C	A	B	C
Cruise 84-9-1									
1	7	81	216*	2	109	189	1	53	97*
5	11	133	275	5	187	313*	1	57	104
11	4	67	91	6	113	172	8	127	215
Cruise 84-9-2									
1	24	44	268	32	97	258	14	137	194
5	22	123	352*	27	139	298	16	118	263*
12	23	61	370	24	79	168*	10	780	182
Cruise 84-10-1									
1	—	—	115	—	—	103	—	—	101*
5	—	—	115	—	—	126	—	—	133
12 (16)	—	—	77*	—	—	186*	—	—	303*
Cruise 85-9-1									
1	10	38	84*	30	75	209	5	53	88
5	23	59	178	21	115	274*	17	90	181*
11	7	71	129	20	86	198	20	60	180
Cruise 85-10									
1	<1	22	72	<1	8	22	<1	22	62*
5	1	36	79*	2	12	45	0	18	46
12 (11)	0.6	23	83	3	27	159*	6	17	128

(Lyczkowski-Shultz et al. 1988). Results of these analyses led to the separation of red drum larvae into three size categories: <2 mm, >2 to ⩽4 mm, and >4 mm, based on diet composition. Column A in Table 4, "preferred" prey, is the combined observed density, from field collections, of those taxa of calanoid and cyclopoid copepods found to most uniquely describe the diet of larvae of the size indicated by the mean lengths listed in Table 3. Crustacean nauplii, column B in Table 4, were the most ubiquitous prey found in red drum larvae of all sizes, and column C is the density of all potential prey items within the size range 63–230 μ, i.e., the total size range of prey found to be ingested by red drum larvae.

In only 6 of 15 vertical data sets did the depth of maximum abundance of larvae coincide with the depth of maximum abundance of their prey. Of the 10 daytime vertical data sets when red drum larvae were most likely to be feeding (Lyczkowski-Shultz et al. 1988), the depth of maximum abundance of red drum larvae coincided with the depth of maximum abundance of their prey in only three instances. In one of those instances, the morning sampling period of cruise 84-10-1, red drum larvae were equally abundant at the depths of lowest and highest observed microzooplankton densities.

Discussion

Red drum larvae ranging in mean size from 1.7 to 5.0mm were vertically stratified in waters of less than 25m of the northcentral Gulf of Mexico. Larvae were most frequently found to be concentrated higher in the water column during the day than at night in vertically well-mixed coastal and inner shelf waters. The lack of a consistent correspondance between depth of maximum larval red drum abundance and depth of maximum prey microzooplankton abundance was not unexpected since, in general, high prey densities (>100 organisms/L) were observed throughout the water column. Brewer and Kleppel (1986) likewise found no correspondance between prey densities and the daytime vertical distribution of northern anchovy and white croaker larvae. The time lag (2–3 hours) between the collection of ichthyoplankton and zooplankton samples may have affected our results if the spatial coincidence of larvae and prey occurred over a shorter time interval than the interval between samples.

It is feasible to assume that red drum larvae maintain this pattern of vertical distribution by responding to diel changes in illumination. In their recent review, Neilson and Perry (1990) concluded that light is important in mediating diel vertical migration in many fishes throughout ontogeny. Diel variations in the distribution patterns of young fishes are associated with activity, phototaxis, and brightness discrimination (Blaxter 1969). Blaxter (1973) was able to induce vertical migration in herring and plaice larvae by varying ambient light levels in the laboratory or by exposing larvae to natural conditions of dawn and dusk. We have observed that 3-5 day-old red drum larvae in the laboratory are positively phototactic and tend to concentrate at the very surface of 4L rearing containers with artifical lighting directly overhead. Larvae were not observed under dark conditions. The range in vertical movement, 5–12m, required to maintain the diel distribution pattern observed in this study is theoretically possible if the swimming capabilities of 2–5mm drum larvae are similar to those of other fish larvae, i.e., with cruising speeds of 2–3 body lengths per second (Blaxter 1969, Theilacker and Dorsey 1980). The role of the swimbladder, clearly visible in red drum larvae by at least 2mm, in "depth holding" (Blaxter 1986) is not known. A comprehensive explanation of how red drum larvae maintain vertical position in the shallow depths of their early nursery grounds requires a more thorough knowledge of early sensory and locomotor capabilities in this species.

The pattern of diel vertical distribution displayed by red drum larvae, implying nocturnal descent, has been termed "reverse diel vertical migration" and has been observed by various workers (Wood 1971, Richards and Kendall 1973, Ohman et al. 1983, Kuwahara and Suzuki 1984, Boehlert et al. 1985, Yamashita et al. 1985, Leis 1986, Sogard et al. 1987). From their review of the literature on vertical migration among fishes, Neilson and Perry (1990) found this pattern to be less common than nocturnal ascent, often associated with similiar movements of prey species, and implicated in reducing predation pressure. Yamashita et al. (1985) attributed this distribution pattern among Japanese sand lance larvae to daytime feeding activity in the upper levels of the water column. The authors suggested that when feeding stops after dark, larvae become relatively inactive and gradually sink to greater depths; with the return of daylight, feeding resumes and larvae move upward.

Activity levels among fish larvae are associated with diurnal light changes and phototaxis (Blaxter 1969). The threshold light intensity found to initiate vertical movement of herring and plaice larvae in the laboratory was similiar to the light threshold for feeding (Blaxter 1986). It would be advantageous for larvae such as red drum living in turbid coastal waters to move into more brightly illuminated levels to feed, given the poor visual acuity and limited retinomotor response capabilities (light/dark adaptation) found in the early larvae of most marine fishes (Blaxter 1969).

Prior to this study, vertical distribution of red drum larvae in the Gulf of Mexico had only been described for estuarine/bay systems. Peters and McMichael (1987) never found red drum larvae at the surface during daytime hours in 1m plankton net collections in Tampa Bay, Florida, where red drum larvae were found to be most abundant nearest the bay mouth. Collections at the bay mouth, however, were taken only at night during a flood tide. The most extensive data on vertical distribution of red drum larvae comes from Aransas Pass tidal inlet on the southern Texas coast where vertical position appears to be influenced by direction of tidal flow (Holt et al. 1989). Further observations and data indicate that high surface densities are generally associated with flooding conditions and/or oceanic water, while high bottom densities occur during ebbing conditions and/or in bay water (S.A. Holt, Mar. Sci. Inst., Univ. Texas at Austin, Port Aransas, TX 78373, pers. commun. Aug. 1990). Tides along the south Texas coast are principally diurnal, and during the red drum spawning season, the flood tide generally occurs at night while the ebb tide occurs during the day.

The relative proportion of the larval red drum population occurring below maximum sampling depths during our study is unknown, but presumed to be small (Comyns et al. 1991). Observations taken during a yearlong survey of Mississippi Sound and adjacent coastal

waters also suggest that red drum larvae, at least during daytime and under flooding conditions, do not occur in large numbers in nearbottom waters of the study area (Lyczkowski-Shultz and Richardson, unpubl. data). Monthly daytime plankton collections were taken from November 1979 to October 1980 at 16 sites inside Mississippi Sound (mean depth 3.9 m), in three tidal passes (mean depth 7.2 m), and at two sites outside the Sound located 7.4 km south of Horn and Petit Bois Islands (mean depth 15.6 m). At each location two depth strata, surface to midwater and midwater to within 0.5 m of the bottom, were sampled separately with stepped oblique hauls of an opening/closing meter net (Lyczkowski-Shultz et al. 1990). Red drum larvae ranging in size from 2.0 to 8.5 mm from 88 collections at all sampling sites combined were more than twice as abundant in the upper half of the water column as in the lower half. This difference was even more pronounced at the two sites outside the Sound where the mean density of larvae (number/100 m^3) was 12.3 in the surface stratum and 4.0 in the bottom stratum. Unlike red drum larvae, the larvae of Atlantic croaker *Micropogonias undulatus* and spotted seatrout *Cynoscion nebulosus* from this same series of collections were more than twice as abundant in the lower half of the water column as in the upper half.

Although the Mississippi Sound and adjacent waters survey was not designed to investigate the role of tide on the distribution of red drum larvae, data from the three barrier island pass stations did tend to support the Aransas Pass inlet observations. Ebbing flow prevailed during sampling at the pass stations only twice during the months when red drum larvae were collected (September and October), and the only instance when drum larvae were more abundant in nearbottom (9 larvae/100 m^3) than in surface waters (0 larvae) occurred during one of those ebb tide collections in Petit Bois Pass. The density of red drum larvae at the offshore station directly south of this pass and under the same ebbing tide, however, was almost three times higher in the surface stratum than in the nearbottom stratum. Our observations from coastal and inner shelf waters during 1984 and 1985 also indicate that tidal stage has little influence on vertical position of red drum in offshore waters.

The vertical distribution of larvae found on cruise 84-10-1 was the only data set that deviated from this generalized pattern. Larvae were concentrated at 12 m during both afternoon and night sampling periods. On the morning of the second day, mean density at 1 and 16 m was the same, suggesting that only a portion of the larval red drum population had moved upward or that the population was still in the process of moving upward. Collections during this cruise contained many large larvae (>4.0 mm) and the night-to-day catch ratio indicated that twice as many larvae were caught during nighttime as in daytime collections. Gear avoidance alone does not explain the absence of larvae at 1 and/or 5 m early in the cruise. The catch ratio for cruise 85-9-1, when larvae >4.0 mm were numerous in collections (Table 3), was 0.2, indicating that more larvae were captured in the daytime.

Local conditions in biological and physical environments can modify diel vertical migration patterns among fish larvae (Neilson and Perry 1990). The "anomalous," deeper daytime distribution of red drum larvae early in cruise 84-10-1 may have been related to local environmental conditions. There are no data on which to assess the influence of predator distributions during this study, and there was no apparent coupling between red drum larvae and their prey. Variations in tidal phase or times of sunrise and sunset do not account for the different pattern observed during cruise 84-10-1. Tidal phase was about the same during all three cruises in 1984 (Fig. 2), and the differences in time of sunrise and sunset between sampling dates in September and October were small, only 17 and 36 minutes, respectively. Temperature and salinity profiles during this cruise were indicative of a homogeneous water column.

Meterological conditions may have been in part responsible for the distribution pattern observed during cruise 84-10-1. On both the day preceding and the first day of this cruise, skies were overcast and rainy with winds in excess of 15 knots; whereas on the morning of the second day, and during all other cruises of our study, skies were clear and winds generally were light. Heath et al. (1988) investigated the effects of sea-surface light intensity and wind stress on the vertical distribution of herring larvae. He found larval aggregation at depth to vary at about the same frequency as light intensity, i.e., diurnally; whereas mean population depth (center of density) was most influenced by wind-induced mixing, with larvae being found deeper in the water column at times of higher wind stress. Weather conditions may also have affected the vertical distribution pattern observed during cruise 84-9-2. Winds during this cruise were light, but for prior days winds had been greater than 10 knots. Although larvae were more abundant higher in the water column in the daytime than at night, the diel changes in maximum abundance extended deeper than in the previous cruise, occurring between 5 and 12 m, instead of 1 and 5 m (Fig. 2B).

Characterization of any dynamic biological process such as vertical migration is constrained by sampling design and gear (Pearre 1979). Plankton nets do not, for example, yield information on whether movement within a population is synchronous or asynchronous, or whether rates of ascent and descent differ among segments of the population. Contradictory observations

or deviations from a proposed pattern can result from sample "snapshots" being taken at different times of an ongoing process. Use of a current drogue as a reference marker for the collection of plankton samples in our study increased the probability of staying with, and repeatedly sampling, a particular patch of red drum larvae. This was clearly the case in cruise 84-9-1, when both larval abundance and size composition remained essentially unchanged throughout the duration of the cruise. Use of a reference marker does not, however, invariably ensure that a particular population will continue to be sampled. During cruise 85-9-1, the change in size composition of larvae in the morning sampling period indicated that a different patch of larvae was being sampled. Nonetheless, a drifting or Lagrangian sampling design would be more likely to yield an accurate description of diel vertical movements than the more typical ichthyoplankton survey design where collections are made at varying times and locations. Sampling designs based on fixed stations are more appropriate for resource surveys when observations from large geographic areas encompassing all or most of a species' spawning grounds are needed to estimate spawner biomass from the abundance of eggs and/or larvae.

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