DIEL-DEPTH DISTRIBUTION OF SUMMER ICHTHYOPLANKTON IN THE MIDDLE ATLANTIC BIGHT

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ABSTRACT

A series of discrete depth plankton tows made every 3 h over a 72-h period off Ocean City, Maryland, in July 1974 allowed analysis of the diel-depth distribution of ichthyoplankton. Overall egg and larval densities averaged 5.6 eggs/m^3 and 6.3 larvae/m^3. Seven species of eggs made up over 90% of those caught with *Merluccius bilinearis* eggs accounting for 45.9% of the eggs taken. Over 16 species of fish larvae were identified, of which *Urophycis* sp., *Pomatomus saltatrix*, and *Citharichthys arctifrons* were the most abundant. The fish eggs were concentrated near the surface and their age distribution at different times of day provided information about diel spawning times, spawning depth, and embryonic mortality. Larvae of all species moved to shallower depths at night. The actual depth distribution and extent of vertical movements varied among the species. The surface and the thermocline were the primary water column features to which diel movements were related.

Studies of the diel vertical distribution of early stages of fish contribute to knowledge of several phases of their life history. For eggs, diel and depth differences in age distribution can be used to estimate time of day and depth of spawning and hatching, rate of embryonic development, and to some extent egg mortality. For larvae, a large body of literature has confirmed the conclusions of the early work by Russell (1926) and Bridger (1956) that most species exhibit diel vertical migrations. Although the depth ranges differ, most species move to shallower depths at night. In some species, e.g., herring, *Clupea h. harengus*, (Seliverstov 1974) and yellowtail flounder, *Limanda ferruginea*, (Smith et al. 1978) the extent of movement increases as the larvae grow. Speculation about causes of vertical migration has centered around diel feeding behavior and predator avoidance. Most larval fishes are visual feeders on zooplankters, which undertake vertical migrations similar to those of larval fish. In addition, Zaret and Suffern (1976) concluded that vertical migration patterns occur in prey species that are vulnerable to visually dependent predators; thus, larvae may reduce predation by moving to deeper water during the day.

Aside from understanding the biological consequences of vertical distribution of larval fishes, the effect this distribution has on results of broad-scale ichthyoplankton surveys is critical. During most such surveys, samples are taken at more-or-less random times during a 24-h day at stations that are separated by tens of kilometers. Depending on the sampling procedures, the diel spawning and embryonic developmental cycle and the diel vertical distribution of larvae may affect interpretation of catches from surveys (Ahlstrom 1959; Miller et al. 1963). If sampling fails to include the entire depth range of the taxa sought, errors in abundance estimates will be made.

METHODS

After making several trial tows at varying distances from shore between Sandy Hook, N.J., and Ocean City, Md., we located a concentration of fish larvae 95 km off Ocean City (lat. 38°32′ N, long. 73°52′ W) in 57 m of water (Figure 1). Earlier studies (Kendall and Walford 1979) indicated that larvae of bluefish, *Pomatomus saltatrix*, which were among those found here, occurred primarily near the surface, above the thermocline. To track the concentration of larvae we deployed a parachute drogue with a lighted staff buoy and the parachute centered at 5-10 m in the layer above the thermocline which was present from 10 to 30

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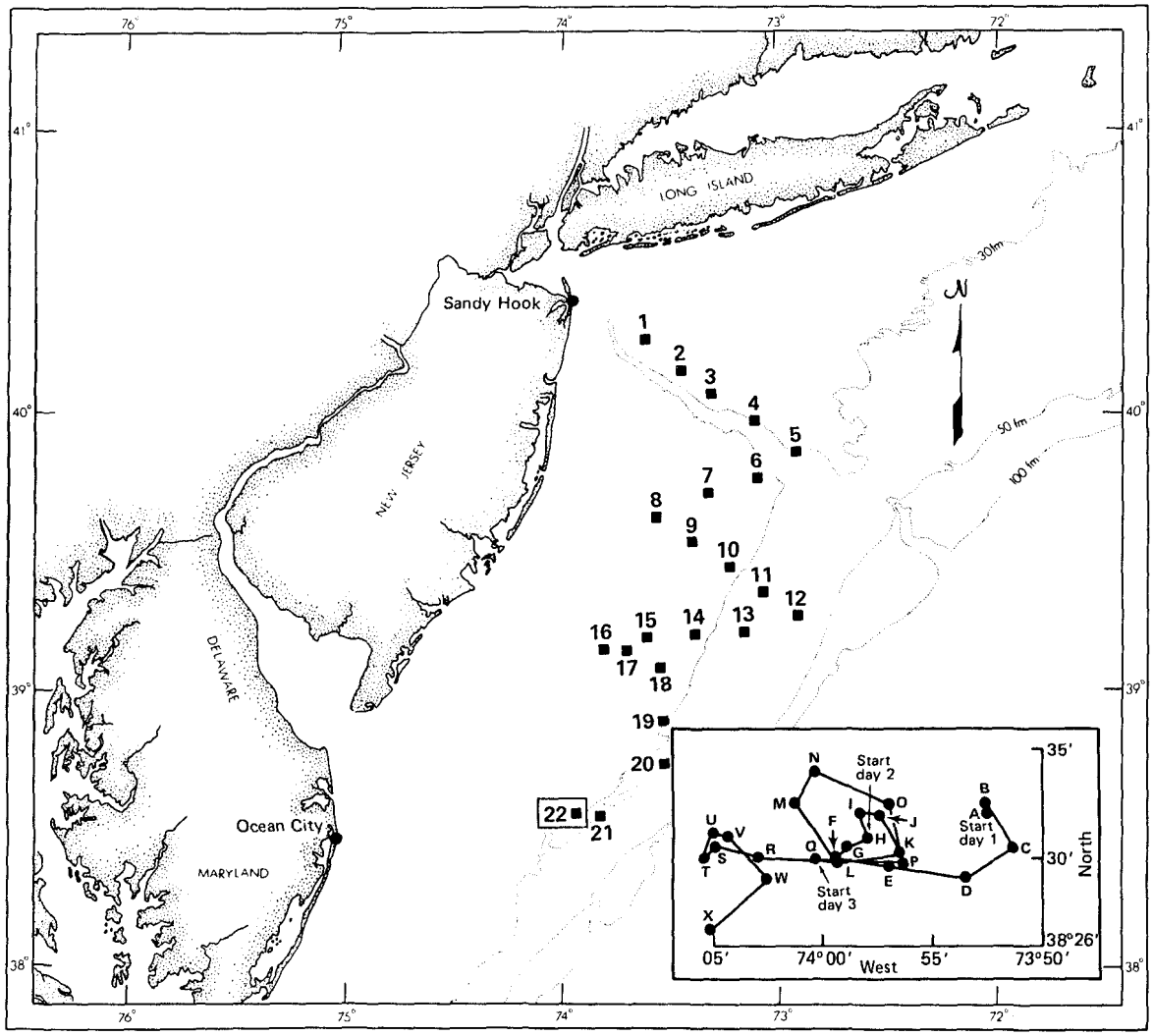

FIGURE 1.—Search (squares) and drogue stations (inset) during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

m. Plankton was sampled near the drogue at 3-h intervals for 72 h starting at 0600 (e.s.t.) on 18 July 1974. We used 20 cm bongo nets equipped with General Oceanics[3] flowmeters and 0.505 mm mesh nets. This mesh size may have caused extrusion of smaller larvae and eggs. Two or four nets were fished simultaneously at discrete depths. A Braincon 6-ft (1.82 m) V-fin depressor was used and wire stops held the nets at predetermined places on the wire.

Before each tow, temperature profiles were obtained with expendable bathythermographs and surface salinity samples were taken. Before every other haul salinity samples from the sampling depths and 50 m were obtained. Salinities were determined on shore with a Beckman RS 7B induction salinometer.

Nominal plankton sampling depths were: surface, 2, 4, 6, 15, and 30 m. Every 3 h a haul was made at 0, 4, 15, and 30 m (first experiment). During the second half of the 72-h period, on every other haul a second haul was made in a similar manner immediately after the first one with the

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

nets fishing at 2 and 6 m (second experiment). The depth stratum from 30 m to the bottom (57 m) was not sampled, and some larvae probably occurred in this area. Bendix bathykymographs on the wire near the subsurface nets checked the actual sampling depths on each haul. During each haul we placed the nets on the wire as it was paid out; the vessel maintained minimal headway to keep the nets from tangling around the wire. Once the nets were on the wire, the vessel speed was increased to 5 kn (9.3 km/h). Hauls lasted 15 min from the time the surface net started to fish to when it was brought out of the water. At the end of the 15 min, the ship was set adrift and the nets were hauled in as quickly as possible. Since the nets had no opening-closing devices, this procedure minimized contamination of the deeper nets by organisms in shallower water. Such contamination was considered inconsequential since the horizontal towing distance was a nominal 2,325 m, and maximum towing distance in shallower layers for the 30 m net was judged to be 75 m (3.2% of the haul); however, it may have accounted for some of the predominantly shallow-caught larvae found in the deeper nets. Samples were preserved in 5% seawater buffered Formalin. The bongo nets provided paired samples that we designated port and starboard. All starboard net samples and one of the four or six port net samples from each sampling time were brought ashore. All fish eggs and larvae were removed from the plankton samples, identified, and counted.

Selected samples of Atlantic whiting,[4] *Merluccius bilinearis*; Gulf Stream flounder, *Citharichthys arctifrons*; and snake eel, *Pisodonophis cruentifer*, eggs were staged (categorized according to developmental stage), based on divisions of the embryonic period used by Naplin and Obenchain (1980). Although many of the early stage eggs had ruptured yolks, these were considered intact prior to sampling. As has been noted in other species (Leis 1977), until the blastoderm completely covers the yolk sac, yolk breakage occurs easily and is likely to happen during sampling. Some middle stages, too, were ruptured, but we cannot determine whether they ruptured during sampling or whether they were already dead when collected. As most of the embryos looked normal and undeteriorated other than having a ruptured yolk, these also were considered to have been alive when sampled.

Atlantic whiting eggs were initially staged at all depths for the first day of sampling (39 samples at eight time periods). Predominant stages at a particular time of day were the same regardless of depth, indicating that stages were not stratified with depth. As 95% of the eggs were taken in the surface and 4 m samples, only the surface samples were staged at each time period for the remaining 2 d of sampling. Gulf Stream flounder eggs were staged at all depths for the first day of sampling, and snake eel eggs, which occurred in fewer numbers, were staged at all depths for all 3 d of sampling.

Stokes' law for determining the settling velocity of a particle has been used to estimate the rising velocity of planktonic eggs (English 1961). Stokes' law, applied to this problem states that

$$V = \frac{2}{9} g \frac{[d_1 - d_2]}{\mu} r^2$$

where V = velocity
d_1 = density of egg
d_2 = density of liquid
g = acceleration of gravity
r = radius of egg
μ = dynamic viscosity of liquid.

All values are expressed in the centimeter-gram-second system. Although no measurements of specific gravity of eggs for species discussed here are available, values for other planktonic eggs have ranged from 1.021 for pleuronectid eggs (English 1961) and for eggs of the gadid *Theragra chalcogramma* (Kanoh 1954) to 1.0287 for *Argentina silus* eggs (Schmidt 1906, quoted by Breder and Rosen 1966). We used the 1.021 value in our calculations because a value >1.022 would not permit eggs to float in the upper 10 m where the eggs we took were abundant.

Bluefish larvae from all samples were measured and those from a subset of 28 samples were used for gut content analysis. From each of these samples, 10 fish representing the sample size distribution were examined for gut contents. The number and types of food organisms in the foregut, midgut, and hindgut were noted. Atlantic whiting and Gulf Stream flounder larvae were also measured.

[4]The common name Atlantic whiting is used in this paper for *Merluccius bilinearis* to avoid confusion with hakes (*Urophycis* spp.). Recently the common name of *M. productus* has been changed from Pacific hake to Pacific whiting. We suggest that fish of the genus *Merluccius* be recognized as whitings, a name in common use on the east coast already.

The average volume of water filtered during the hauls was 82.9 m^3 (range 58.6-109.2 m^3). All numbers of eggs and larvae were adjusted to numbers per 100 cubic meters. Using UCLA BMD computer program 02V (Dixon 1973), analyses of variance were performed for several species after the data had been transformed to $\log_{10}(X + 1)$ to normalize the distribution and homogenize the variances, which were proportional to the means before transformation. The factorial design of the first experiment had the following factors: three 24-h days, four sampling depths (0, 4, 15, 30 m), and day and night. Each factor combination had three replicates. Because the cruise was in mid-summer, by sampling every 3 h, three tows were taken each night and five each day. To equalize the number of day and night tows for the analyses of variance, only the first, third, and fifth daytime tows were used. We performed similar analyses on the data associated with the second experiment when collections were also made at the 2 and 6 m depths. For these data the factors were: three times of day (evening—1800 h; night—0000 h; and day—0600 h and 1200 h), and six depths (0, 2, 4, 6, 15, 30 m). Each of these factor combinations had two replicates.

RESULTS

The drogue drifted about 11 nmi (20.4 km) to the west-southwest of its original position during the 72-h sampling period. Three circular patterns that corresponded to a diurnal tidal cycle were evident within the overall drift (Figure 1). During the first half of the experiments the wind was generally southerly at 5-25 kn (9.3-46.3 km/h). The skies were cloudy and a thundersquall occurred around 0300 h on the first night. Around 2100 h on the second night there was another thundersquall, and at 0300 h the wind shifted to north-northwest at 20 kn (37.0 km/h) and the skies cleared. The wind diminished during the third day and by 2100 h it had shifted to southeast at only 2 kn (3.7 km/h). The sky remained clear. The sun rose at 0545 h and set at 2016 h during the experiments. The new moon rose and set during twilight or daylight hours throughout the sampling period, so there was no moonlight at night.

The water column represented three water types characteristic of the continental shelf of the Middle Atlantic Bight. Coastal water above the thermocline at 8 m was isothermal at 22.2°-22.8° C and had salinities of $<33.6‰$ (Figure 2). Below

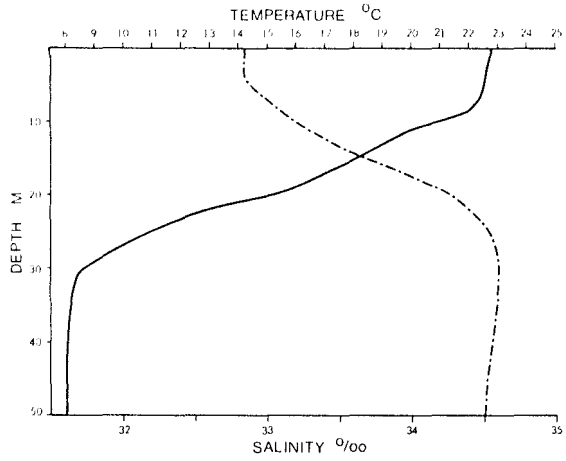

FIGURE 2.—Mean temperature (line) and salinity (dashed line) profiles at drogue stations during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

the thermocline, where temperatures dropped from 21.5° C at 10 m to 8.5° C at 30 m and salinities exceeded 33.6‰, was shelf edge water (Wright and Parker 1976). Near the bottom, where temperatures were <10° C and salinities were 34.5-34.6‰, the water was part of the cool pool that occurs over the middle of the shelf off the Middle Atlantic Bight in summer (Bowman and Wunderlich 1977). The diversity of ichthyoplankton collected was probably due in part to our sampling in these three water types.

A total of 61,534 eggs (an overall arithmetic mean of 562 eggs/100 m^3), most of which were identified to species, were taken during the experiments (Table 1). Most numerous were Atlantic whiting and Gulf Stream flounder. Butterfish, *Peprilus triacanthus*; fourspot flounder, *Hippoglossina oblonga*; hakes, *Urophycis* spp.; snake eel; and cunner, *Tautogolabrus adspersus*, eggs were also taken in significant numbers. No bluefish eggs were taken during the cruise.

Throughout the cruise, egg numbers of all species decreased with depth. Data from the second experiment was similar to that from the first, and showed that the catches at 6 m more closely resembled those at the surface and 4 m than those at 10 and 30 m. These findings indicate that the planktonic eggs of all species taken behave in much the same way in the water column, and have similar specific gravities.

A total of 68,840 larvae (an overall mean of 629 larvae/100 m^3), of which most were identified to

TABLE 1.—Numbers and relative abundance of fish eggs and larvae at the drogue stations during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Taxon	Eggs			Larvae		
	Total number	Mean no./ 100 m^3	% of total	Total number	Mean no./ 100 m^3	% of total
Hakes, *Urophycis* spp.	2,988	27	4.9	15,972	146	23.2
Bluefish, *Pomatomus saltatrix*				15,202	139	22.1
Gulf Stream flounder, *Citharichthys arctifrons*	17,311	158	28.1	13,568	124	19.7
Frigate mackerel, *Auxis* sp.				5,904	54	8.6
Butterfish, *Peprilus triacanthus*	4,497	41	7.3	5,445	50	7.9
Fourspot flounder, *Hippoglossina oblonga*	3,898	36	6.3	5,062	46	7.4
Atlantic whiting, *Merluccius bilinearis*	28,243	258	45.9	3,281	30	4.8
Smallmouth flounder, *Etropus microstomus*				1,000	9.1	1.5
Atlantic bonita, *Sarda sarda*	114	1.0	.2	764	7.0	1.1
Searobins, *Prionotus* spp.				445	4.1	.6
Cusk eels, Ophidiidae				183	1.7	.3
Cunner, *Tautogolabrus adspersus*	2,397	22	3.9	152	1.4	.2
Yellowtail flounder, *Limanda ferruginea*				151	1.4	.2
Eels, Anguilliformes				98	.9	.1
Goosefish, *Lophius americanus*				63	.6	.1
Witch flounder, *Glyptocephalus cynoglossus*				42	.4	.1
Snake eel, *Pisodonophis cruentifer*	2,058	19	3.3			
Miscellaneous[1]	28	.3		1,508	13.8	2.2
Total	61,534	562	99.9	68,840	629	100.1

[1]Animals that were too mutilated to be identified or too sparse for meaningful analysis.

species, were taken during the experiments (Table 1). Hakes, bluefish, and Gulf Stream flounder were most abundant, and frigate mackerel (*Auxis* sp.), butterfish, fourspot flounder, Atlantic whiting, and smallmouth flounder, *Etropus microstomus*, were taken in substantial numbers.

Bluefish

An overall mean catch of 139 larvae/100 m^3 was made placing bluefish second to hakes in abundance. A highly significant difference occurred in the catches among the 3 d, with more larvae caught on day 2 than on the other 2 d (Table 2). More larvae were taken in the surface and 4 m nets than at other depths, with more taken at the surface at night than during the day (Figures 3, 4). Both day and night catches at 15 and 30 m were so small that they may have been a result of contamination of the nets as they passed through shallower water. During the second experiment, the larvae were concentrated at 2 m at night and 6 m at other times (Table 2).

The vertical-diel migration of these larvae is clearly seen by comparing the proportions of larvae in the 0 and 4 m tows at each time of day sampled (Figure 4). The proportion in the surface tow was lowest at midday (1200 h) when it was 4% of the total catch. It increased steadily to 49% of the catch at midnight (0000 h) when it started to decline again, reaching 17% by midmorning (0900 h). Thus the larvae appear to be varying their depth distribution continuously on a diel cycle, concentrating near 4 m during midday and at the surface at night.

The percentage of the larvae with food in their guts also showed a marked diel pattern (Figure 4). The maximum proportions of larvae with food in their guts were taken from 0600 to 1200 h when 86-90% of the guts contained food. At 1500 and 1800 h, 70% of the larvae contained food. By 2100 h the proportion had dropped to 22% and during the night (0000 and 0300 h) none of the larvae had food in their guts.

Most of the food consisted of various life stages of copepods, including nauplii, copepodites, and adults. Cladocerans and invertebrate eggs were also present in small numbers. It also appeared that smaller larvae had higher proportions of nauplii while larger larvae had higher proportions of adult copepods and cladocerans although too few fish were examined for detailed analysis.

Several factors indicate that food passes through the gut fairly rapidly. Few fish had any food particles in the foregut. At 0600 h about twice as many larvae had food in the midgut as had food in the hindgut. Later in the day about equal numbers of larvae contained food in the midgut and in the hindgut. At no time did more hindguts than midguts contain food.

The mean lengths of bluefish larvae were compared among the tows. The mean length for all tows was 4.33 mm (Table 3). We found no significant difference in mean lengths among the 3 d of sampling, between day and night sampling, or among the six sampling depths. Larger larvae

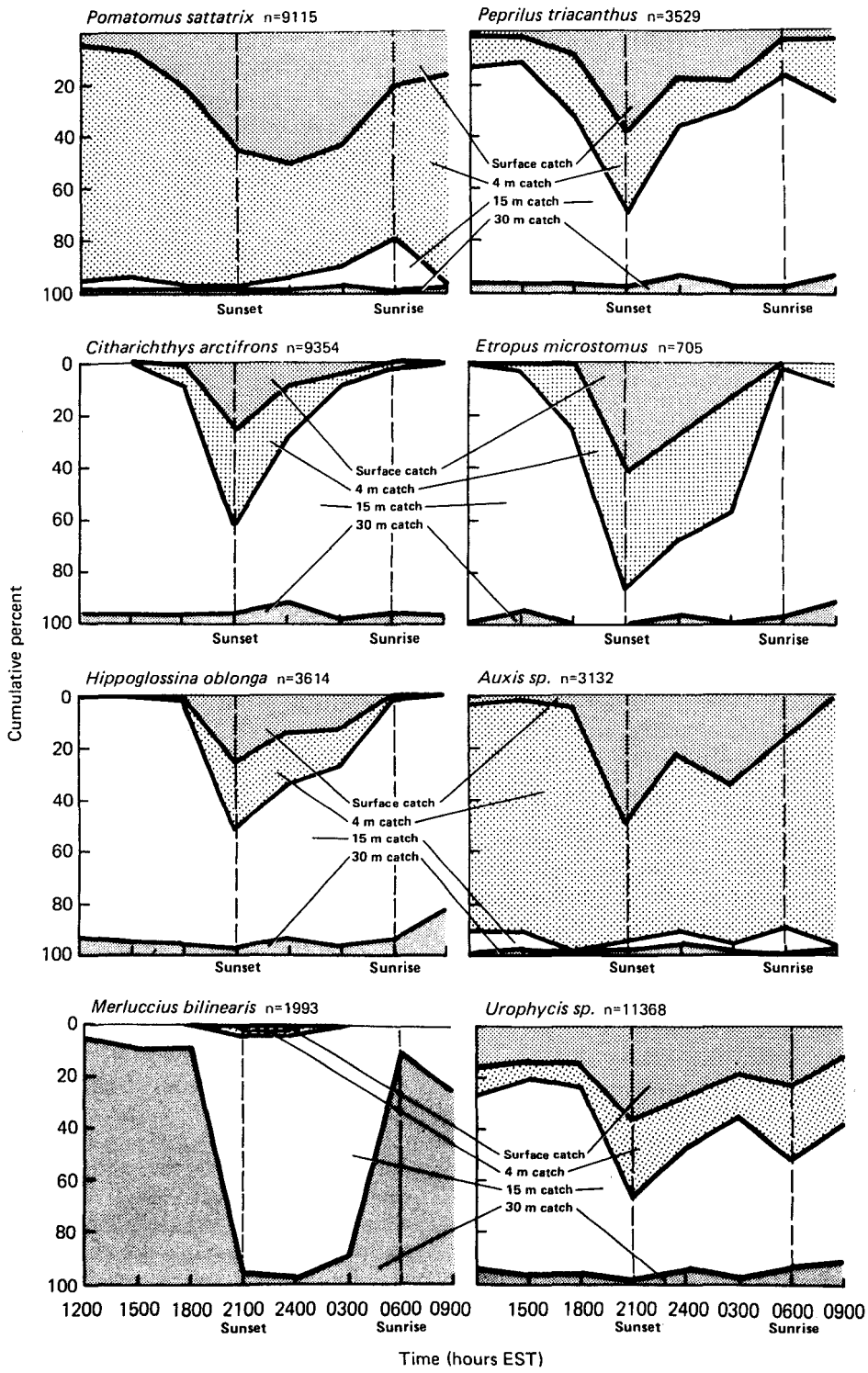

FIGURE 3.—Mean proportions of larvae of eight species of fish at four depths over a 24-h cycle from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

TABLE 2.—Transformed ($\log_{10} X + 1$) mean numbers of larvae per 100 m^3 and F-values from analysis of variance for eight species of fish taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Item	Bluefish	Atlantic whiting	Gulf Stream flounder	Butterfish	Fourspot flounder	Hakes	Frigate mackerel	Smallmouth flounder
Experiment 1: depths = 0, 4, 15, 30 m; times = day, night; days = 1, 2, 3								
Means:								
Overall	1.550	0.786	1.311	1.315	1.088	1.904	1.056	0.524
Day	1.497	.692	1.105	1.222	.799	1.885	.880	.392
Night	1.603	.880	1.518	1.408	1.378	1.923	1.233	.656
Day 1	1.289	.819	1.215	1.334	1.024	1.945	.793	.199
Day 2	1.717	.879	1.287	1.287	1.006	1.859	1.238	.538
Day 3	1.644	.660	1.432	1.325	1.235	1.907	1.138	.835
Depths:								
0	1.847	.150	.835	1.087	.791	2.005	1.222	.445
4	2.375	.266	1.075	1.400	.846	1.916	1.870	.658
15	1.210	1.404	2.193	1.391	1.849	2.378	.728	.801
30	.768	1.323	1.143	.843	.867	1.318	.405	.191
F-values								
Days	12.32**	3.77*	1.32	.09	3.33*	.43	11.45**	25.40**
Day-night (diel)	1.99	7.89**	13.72**	3.80	51.63**	.26	19.74**	13.22**
Depth	88.13**	99.32**	29.19**	24.14**	39.88**	33.74**	64.43**	13.31**
Days/Day-night	1.35	3.49*	.40	.20	.72	.54	2.53	5.58**
Days/Depth	1.02	.13	1.20	1.06	3.65**	1.10	2.06	2.70*
Day-night/Depth	6.96**	4.88**	13.49**	5.70**	29.57**	2.85*	6.89**	13.16**
Days/Day-night/Depth	1.72	.30	.81	.42	1.36	1.89	1.31	1.80
Experiment 2: depths = 0, 2, 4, 6, 15, 30 m; times = 1800, 0000, 0600-1200 h								
Means:								
Overall	1.954	.523	1.280	1.348	1.073	1.909	1.422	.740
Times:								
1800	1.945	.524	1.388	1.570	0.818	1.810	1.521	1.019
0000	1.965	.591	1.612	1.375	1.458	1.892	1.598	.638
0600-1200	1.952	.453	.840	1.100	.942	2.023	1.146	.563
Depths:								
0	1.839	.064	.633	.884	.459	1.946	.941	.361
2	2.295	.115	1.308	1.362	1.223	2.000	2.026	.958
4	2.471	.244	.994	1.410	.615	1.847	1.931	.731
6	2.628	.244	1.154	1.552	1.043	2.016	2.179	.809
15	1.552	1.117	2.260	2.065	2.176	2.388	.984	1.288
30	.939	1.351	1.331	.817	.920	1.254	.468	.294
F-values								
Time of day	.02	.74	10.36**	12.02**	10.46**	2.25	7.69**	5.92
Depth	30.85**	2.48	9.73**	22.90**	16.80**	13.32**	33.32**	6.90**
Time/Depth	2.63*	8.54**	4.49**	5.08**	3.17*	1.27	3.89**	4.80**

*P = 0.05; **P = 0.01.

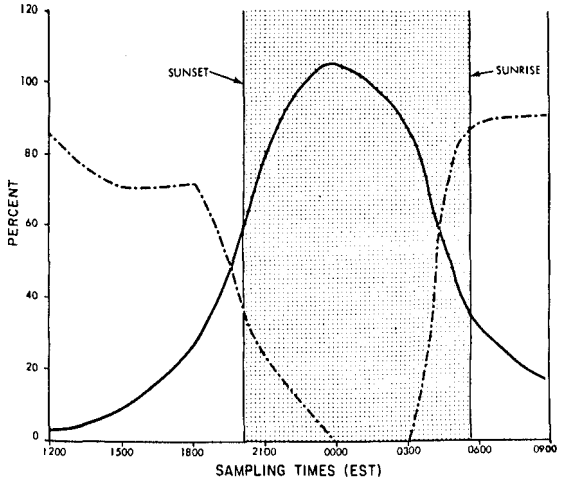

FIGURE 4.—Mean percentage (surface/4 m) of bluefish larvae in the 4 m tow relative to those in the 0 m tow (line) and percentage of bluefish larvae with food in their guts (dashed line) by time of day from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

TABLE 3.—Mean standard lengths (millimeters) of bluefish larvae taken at various times of day and depths during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Depth (m)	Day 1		Day 2		Day 3		All times
	Day	Night	Day	Night	Day	Night	
0	5.30	4.38	4.57	4.25	4.87	4.69	4.57
2			4.38	4.45	4.60	4.85	4.59
4	4.38	4.52	3.89	4.45	4.27	4.63	4.22
6			4.27	4.42	4.25	4.79	4.33
15	4.65	4.45	4.49	4.42	4.31	4.71	4.47
30	4.57	4.61	4.45	4.35	4.25	4.50	4.45
	Day 1 - 5.00		Day 2 - 4.18		Day 3 - 4.46		
	Day - 4.25		Night - 4.54		Overall - 4.33		

showed no increased net avoidance during daylight, nor any difference in depth distribution with size. The apparent lack of larval growth over the 72-h sampling period may be related to the difference between the drift of bluefish larvae and that of our drogue.

Since bluefish egg incubation takes about 48 h

at temperatures near 22° C (Salekhova 1959; Deuel et al. 1966) and bluefish larvae hatch at about 3.0 mm, the larvae we caught averaging 4.3 mm were probably several days old. Apparently bluefish spawned rather steadily over a period of several days somewhere "upstream" from our drogue a few days prior to our experiment, and the larvae drifted continuously through our sampling area. Alternate hypotheses that the larvae did not grow during the experiment, or that larvae >4.3 mm avoided the nets, do not seem as tenable.

Atlantic Whiting

Atlantic whiting eggs were the most numerous among the species taken, with an overall mean of 258 eggs/100 m^3 taken during the cruise. All three primary factors (depth, time of day, and days) showed significant differences: egg number decreased with increasing depth (Figure 5), more eggs were taken at night than during the day, and significantly fewer eggs were taken on the second sampling day than on the other two (Table 4).

The uneven distribution of various developmental stages over time allows separation of eggs into distinct groups or batches whose development can be traced from spawning through hatching (Table 5). At each sampling time, eggs from two distinct batches were taken which apparently represented the daily spawning products of adults in the area. Very early stages appeared daily in the afternoons from about 1500 to 1800 h. These eggs continued developing throughout the next day and began hatching at 0300 h the second day after being spawned. After 0900 h, virtually all eggs had hatched. Therefore, the total incubation time at the surface temperature we observed, 22.2°-23.2° C (mean = 22.7° C), was about 39 h.

TABLE 4.—Transformed ($\log_{10} X + 1$) mean numbers of eggs per 100 m^3 and F-values from analysis of variance for six species of fish taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Item	Atlantic whiting	Gulf Stream flounder	Butterfish	Fourspot flounder	Hakes	Snake eel
Experiment 1: depths = 0, 4, 15, 30 m; times = day, night; days = 1, 2, 3						
Means:						
Overall	1.971	2.059	1.180	1.228	1.056	0.907
Day	1.892	1.996	1.052	1.259	.985	.864
Night	2.051	2.122	1.307	1.197	1.128	.950
Day 1	2.058	1.888	1.090	.944	1.053	.831
Day 2	1.867	2.110	1.255	1.336	.998	.861
Day 3	1.988	2.179	1.194	1.403	1.119	1.029
Depths:						
0	2.640	2.251	1.575	1.677	1.521	1.271
4	2.606	2.205	1.670	1.685	1.582	1.494
15	1.552	1.887	.950	.755	.700	.650
30	1.086	1.893	.524	.973	.423	.212
F-values						
Days	4.19*	14.76**	.76	31.87**	.62	5.88**
Day-night (diel)	8.46**	7.62**	5.36*	1.49	2.59	2.92
Depth	201.63**	18.31**	24.13**	106.64**	43.33**	132.38**
Days/Day-night	1.11	2.21	2.26	.32	3.29*	3.19
Days/Depth	.19	4.46**	.43	2.13	1.08	2.58*
Day-night/Depth	1.08	2.84*	.19	.58	.28	3.58*
Days/Day-night/Depth	.52	.19	.25	.66	.74	3.35**
Experiment 2: depths = 0, 2, 4, 6, 15, 30 m; times = 1800, 0000, 0600-1200 h						
Means:						
Overall	2.142	2.217	1.366	1.548	1.250	1.166
Times:						
1800	2.141	2.165	1.598	1.546	1.146	1.163
0000	2.225	2.348	1.595	1.514	1.336	1.107
0600-1200	2.061	2.138	.904	1.584	1.267	1.228
Depths:						
0	2.561	2.331	1.591	1.831	1.510	1.109
2	2.537	2.405	1.691	1.822	1.563	1.680
4	2.537	2.295	1.601	1.848	1.655	1.544
6	2.590	2.382	1.783	1.815	1.645	1.624
15	1.554	2.007	1.088	1.010	.764	.875
30	1.076	1.882	.440	.963	.361	.165
F-values						
Time of day	4.30*	8.68**	27.96**	.27	3.53	.75
Depth	139.11**	15.77**	23.07**	21.53**	57.70**	35.30**
Time/Depth	3.52*	1.67	2.00	.56	2.91*	1.41

*P = 0.05; **P = 0.01.

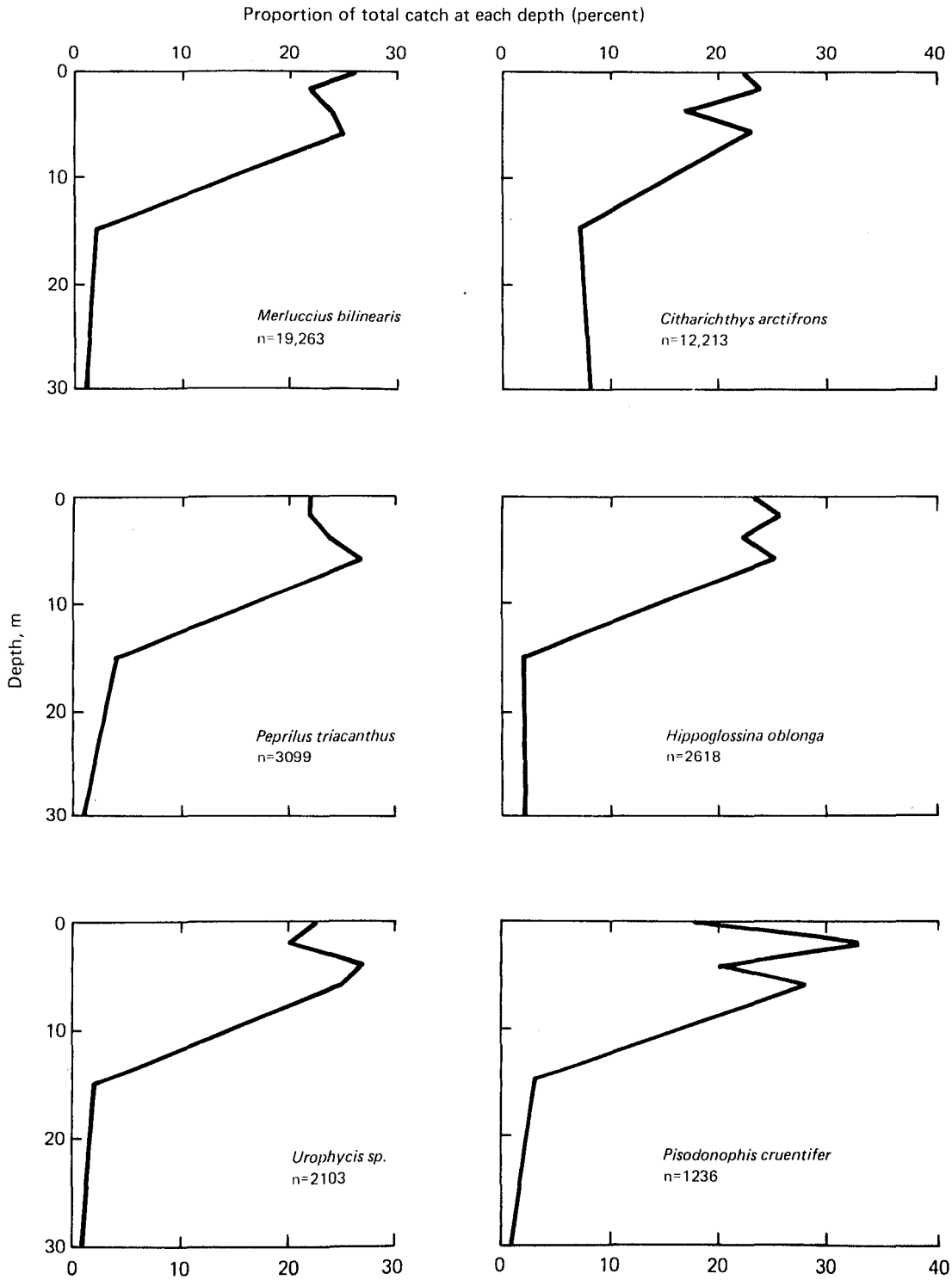

FIGURE 5.—Depth distribution of planktonic eggs of six species of fish collected during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

TABLE 5.—Stages of Atlantic whiting eggs taken in surface samples during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight. Roman numerals refer to batch numbers that were assigned to eggs.

Stage	Drogue station: / Time:	A 0600	B 0900	C 1200	D 1500	E 1800	F 2100	G 2400	H 0300	I 0600	J 0900	K 1200	L 1500	M 1800	N 2100	O 2400	P 0300	Q 0600	R 0900	S 1200	T 1500	U 1800	V 2100	W 2400	X 0300
Precell	III			1	49	26	6				IV	3	44	2					V	3	28	1			
2 cell					13	3	4						11	3							17				
4 cell					1		6						3								2				
8 cell							1														1	2			
16 cell	II					5	1														3	22			
Cell stage					5	28	7						15	53	5	22					11	22	4	1	
Early blastula		9	1		1	58	23	4	5	2				37	13	15	12	4	1		1	177	14	24	3
Blastodermal cap		7	1	1	1	32	161	19	5	5				16	121	29			1			63	183	28	94
Early germ ring		9	4	1		8	39	345	22	19					10	142	18	8				2	12	182	93
Germ ring ½ down		58	5	1	1		1	59	89	17	3					2	95	25	8	3			1	4	554
Germ ring ¾ down		46	21	2					283	15	5	1				1	54	42					1		198
Blastopore almost closed		28	31						176	25	16						3	11							9
Early middle		106	71	26					23	401	36	8					1	85	19	18	4				
Middle middle		54	164	51	19	1				40	380	23	3	1				1	107	12	25	2			
Late middle		1	37	137	44	9	1				42	79	29	2					7	155	67	19	1		
Early late				45	15	11					1	5	30	5						13	34	15	2		
Tail ⅝ around yolk	I	1		8	148	31	11	3				5	70	41	4						261	66	8	7	6
Tail ¾ around yolk		1		2	23	124	42	7					4	105	32	4	1				12	200	56	14	8
Tail ⅞ around yolk		8				10	170	47	4		1			4	98	13	6					6	160	99	35
Full circle		29	7				6	86	26	28					3	22	10	3					3	116	57
Tail 1⅛ around yolk		58	38	3				13	86	47	6	1			1		17	8	6					2	57
Abnormal late		6	2			20	14	21	4	5			1	2	1	30	14	16		2		2	9	12	7
Total		421	382	278	320	366	493	604	723	604	490	125	210	271	288	280	231	203	149	206	466	599	454	489	1,121

Kuntz and Radcliffe (1917) found that development in the laboratory required "not over" 43 h, but did not give temperature data.

During the cruise, all the eggs collected were spawned on 5 different days. Those spawned during the afternoon of the first sampling day (batch III) were the only ones sampled from spawning to hatching.

Batches of developing embryos spent roughly 3 h in each of the developmental stages listed in Table 5, except for the very early cell stages. From these data we derived a timetable of embryonic development (Table 6). Blastopore closure occurred about 12 h after spawning. Eggs were in middle stages of development, i.e., between blastopore closure and first appearance of the tail bud, for about 9 h. Hatching occurred about 15 h after tail bud formation.

The numbers of eggs in each batch are plotted according to developmental stage and time of day in Figure 6. Number of eggs taken varied widely from tow to tow; hence, we could not estimate mortality within any batch. In most tows, however, several obviously malformed late stages occurred in which embryos usually had ruptured yolks and shortened, rather wide tails. We assume that the condition of these embryos was not due to handling. These embryos, which composed up to 5.2% of an egg batch (Table 7), would probably not have survived to hatch.

The numbers of eggs taken at different times of day vary as batches are spawned and as they hatch (Figure 7). Because the eggs are spawned during only one period of the day (1500-1800 h), we would expect the maximum numbers of eggs to occur at

TABLE 6.—Timetable of development of Atlantic whiting eggs based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Time	Hours from spawning	Developmental stage
Day 1:		
1500	0	Precell
1800	3	Cell stage
2100	6	Early blastula
2400	9	Blastodermal cap
0300	12	Early germ ring
0600	15	Germ ring ½-¾ down
0900	18	Early middle
Day 2:		
1200	21	Middle middle
1500	24	Late middle
1800	27	Tail ⅝ around yolk
2100	30	Tail ¾ around yolk
2400	33	Tail ⅞ around yolk
0300	36	Full circle
0600	39	Tail 1⅛ around yolk—hatching
0900	42	Tail 1⅛ around yolk—hatching

about 1800 h; however, we found egg density to increase until 0300 h. The downward slope on the right side of the curves primarily reflects embryonic mortality, although hatching accounts for the decrease during the latest developmental stages. The fact that the egg batches reached their peak abundance later than expected probably reflects the influence of local currents on distribution of spawning adults and eggs.

TABLE 7.—Percentage of abnormal Atlantic whiting embryos in each spawning batch from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Batch	Total no. eggs	No. abnormal late stages	Minimum mortality (%)
I	153	8	5.2
II	2,012	64	3.2
III	3,224	64	2.0
IV	2,624	32	1.2
V	1,760	—	—

Determining the time and depth at which eggs were spawned provides information about adult spawning behavior. We have shown that newly spawned eggs appear in the afternoon and early evening. The depth at which spawning occurs can be estimated from knowing the depth at which the very early stage eggs were collected. Atlantic whiting eggs are planktonic, tending to rise toward the surface at a rate which, aside from turbulence of the water, depends on their specific gravity and that of the surrounding water. Estimating the rate of rise of the eggs in the water column enables us to calculate the depth at which

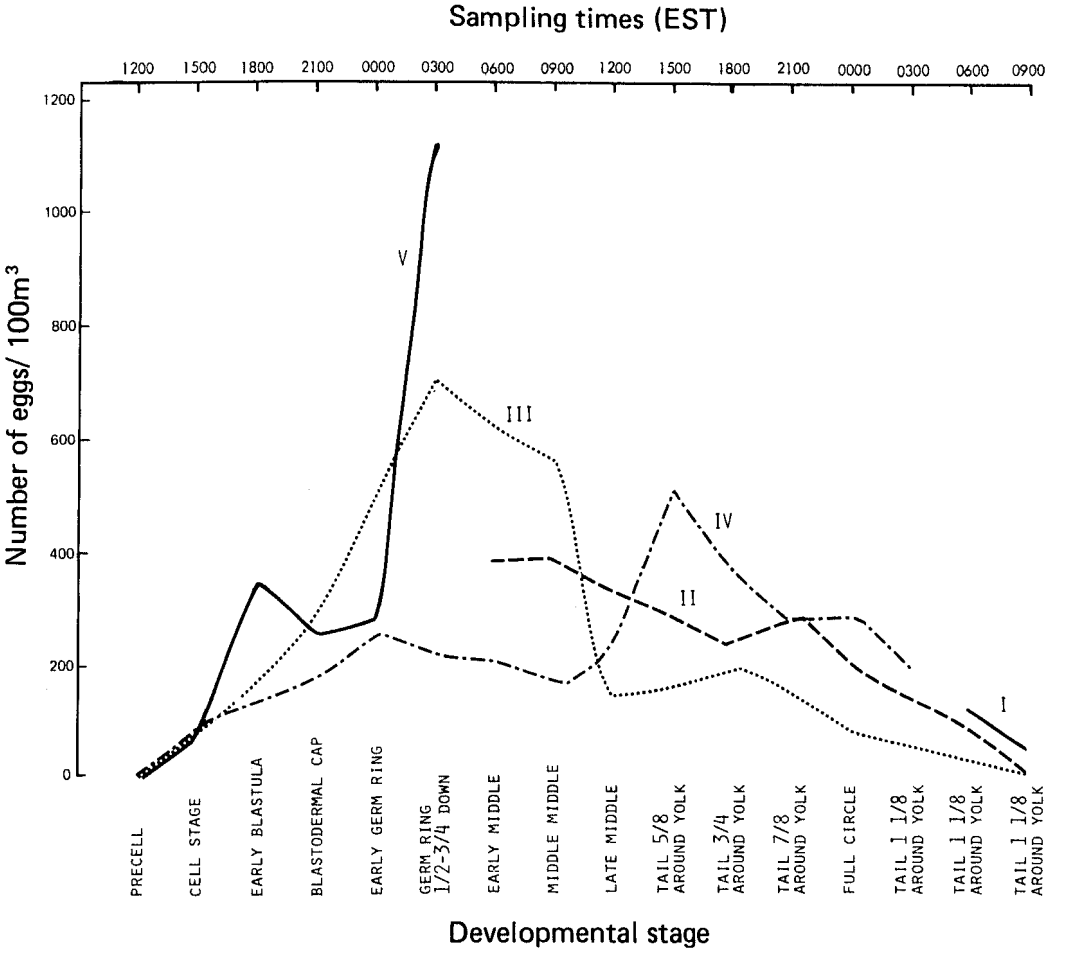

FIGURE 6.—Numbers of Atlantic whiting eggs in the five batches taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974, plotted by developmental stage and time of day.

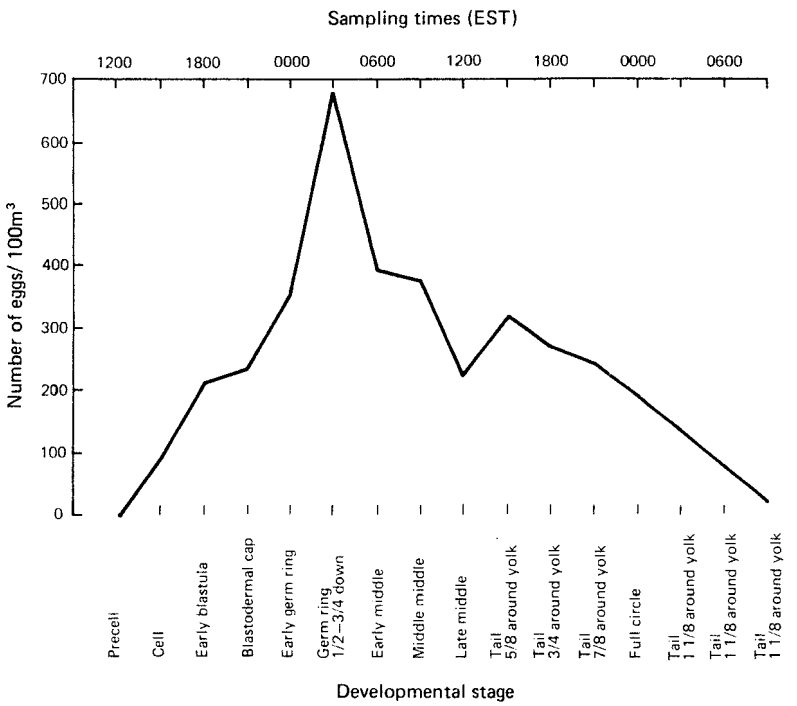

FIGURE 7.—Average number of Atlantic whiting eggs from spawning to hatching plotted by developmental stage and time of day, based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

the eggs were spawned. According to Stokes' law, Atlantic whiting eggs would have a rising velocity of 1.18 m/h or about 3.5 m during the 3-h interval between samples. Based on this and the fact that newly spawned eggs were taken primarily in the 0 and 4 m nets, the adults were spawning in the upper 10 m of the water column.

An overall mean of 30 Atlantic whiting larvae/ 100 m^3 was taken during the cruise. The numbers of larvae showed significant differences for all three primary factors (depth, time of day, and days) (Table 2). In general, the number of larvae caught increased with increasing depth (Figure 3). Significant numbers of larvae may have occurred below our 30 m sampling depth. A comparison of the numbers of larvae taken in the 15 and 30 m tows at various times of day (Figure 8) shows that more larvae were caught at 30 m during the day, while at night many more larvae were taken at 15 m. In general, more larvae were caught at night; however, on day 3 more were taken in the daytime. The larvae either avoided the nets more effectively in the daytime or more larvae migrated upward into the range of the nets at night.

Figure 9 shows the average lengths of larvae caught at 15 m and at 30 m. During the daytime, the 4.5 mm larvae were at 15 m while 6.5-9.2 mm larvae stayed at 30 m. At night, large larvae (6-9 mm) were at both 15 and 30 m, probably mixing with the small larvae, some of which may have sunk between 1800 and 0000 h, based on the decrease in mean length at 30 m and the increase in mean length at 15 m.

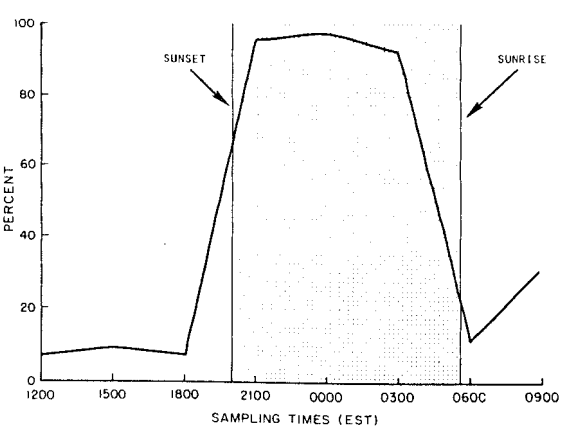

FIGURE 8.—Mean percentage of Atlantic whiting larvae at 15 m relative to larvae at 30 m by time of day from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

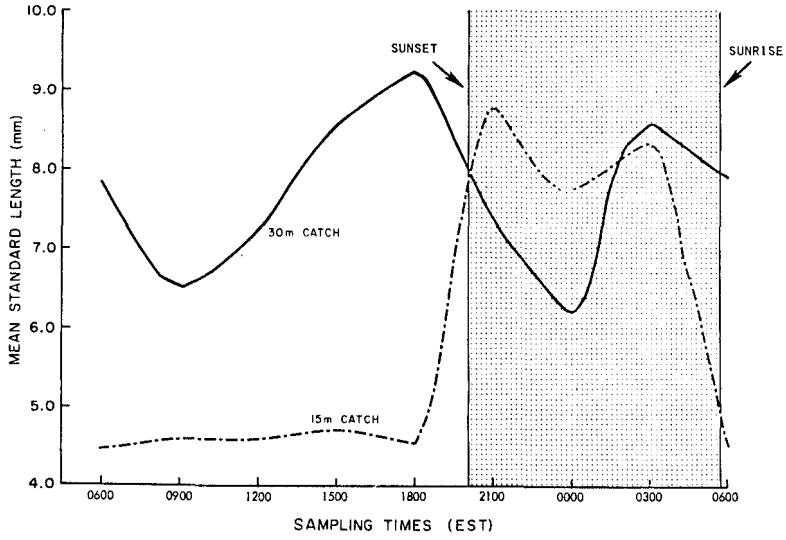

FIGURE 9.—Mean standard lengths (millimeters) of Atlantic whiting larvae taken at 15 and 30 m by time of day from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

We caught very few hatchlings (<3.0 mm [Kuntz and Radcliffe 1917]), as they appear to have been extruded from the 0.505 mm mesh net. Therefore, we could not detect a pulse in the numbers of very small larvae corresponding to the daily time of hatching or shortly thereafter. Significantly fewer larvae of all sizes were taken on day 3.

Gulf Stream Flounder

Gulf Stream flounder eggs have not been fully described in the literature, although Richardson and Joseph (1973) described eggs stripped from Gulf Stream flounder that were approaching spawning condition. The very small larvae are so similar to those of smallmouth flounder, *Etropus microstomus*, that the eggs also may be virtually indistinguishable from that species. In fact, eggs from our samples are identical to those described as smallmouth flounder eggs by Scherer and Bourne (1979), who did not provide adequate means of distinguishing the two species.

We have identified eggs from the plankton that we consider to be Gulf Stream and/or smallmouth flounder eggs based on egg and oil globule diameter and late embryonic characteristics. We assume that such eggs taken during this cruise are Gulf Stream flounder eggs for three reasons. First, Gulf Stream flounder occurs mainly at depths >46 m while smallmouth flounder is most common in water <27 m (Richardson and Joseph 1973); our samples were from an area where the water was 57 m deep. Second, smallmouth flounder larvae occur farther south than Gulf Stream flounder; our sampling location was in an area of peak Gulf Stream flounder abundance, but north of the area of maximum smallmouth flounder concentration (Smith et al. 1975). Finally, Gulf Stream flounder larvae occurred in markedly greater numbers in our samples than did smallmouth flounder larvae (19.7% as opposed to 1.5% of the total catch).

Gulf Stream flounder averaged 158 eggs/100 m^3 during the cruise. The catches were significantly different for all three primary factors (depth, time of day, and day) (Table 3). Fewer eggs were taken with increasing depth (Figure 5), though comparable numbers were taken at 15 and 30 m; more eggs were taken at night; and the total number of eggs increased with each day of sampling. More eggs were taken on each succeeding day at all depths except 30 m, where the number decreased with time.

Gulf Stream flounder eggs showed patterns of developmental stages that changed with both time and depth. Table 8 shows stages of eggs summed over all depths at each sampling time. The eggs were more difficult to separate into batches than Atlantic whiting eggs, but batches were defined in which eggs could be traced from spawning through hatching in succeeding samples. Usually three distinct groups of developmental stages were apparent at each sampling time. Precell stages were taken in the afternoon from 1500 to 2100 h. These eggs required about 3

TABLE 8.—Stages of Gulf Stream flounder eggs taken on day 1 during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974. Roman numerals refer to batch numbers that were assigned to the eggs.

Stage	Drogue station: / Time:	A 0600	B 0900	C 1200	D 1500	E 1800	F 2100	G 2400	H 0300
Precell		IV 1			25	19	5	V	2
2 cell					11	17	8	3	1
4 cell				2	2	15	15	1	
8 cell					2		4	12	
16 cell		2		3			11	1	
Cell stage		11 III	3			2	4	19	4
Early blastula		15	8	6	17	6	18	33	13
Blastodermal cap		86	84	43	17	38	18	41	32
Early germ ring		56	104	83	88	58	25	20	16
Germ ring ½ down		6	13	27	38	37	19	14	3
Germ ring ¾ down		7	9	4	12	17	21	10	3
Blastopore almost closed		9 II	3	6	7	10	8	20	
Early middle		22	15	5	4	4	19	38	8
Middle middle		16	13	8	6	6	6	19	20
Late middle		13	34	9	9	4	2	12	14
Early late		21	21	18	7	4	1	10	8
Tail ½ around yolk		5	11	1	7	4	1	1	2
Tail ⅝ around yolk		18	14	8	25	17	21	7	10
Tail ¾ around yolk		9	8	16	12	14	27	8	8
Tail ⅞ around yolk		11 I	6	7	15	15	16	32	10
Full circle		5	8	5	3	4	2	4	4
Total		312	355	251	307	291	251	305	158

full days to hatch; hatching occurred primarily in near-surface water beginning around 0900 h the morning of the fourth day after spawning.

Staging the eggs also revealed that they were stratified with depth, with early stages being taken in the deeper nets (Figure 10). Precell stages were taken primarily at 30 m, while eggs with several cell divisions and early blastula and blastodermal cap stages were taken mainly at 15 m. From 0900 to 1200 h the morning after spawning, early germ ring stages gradually shifted from 4 m to the surface. After 1200 h, the later stages were found at all depths sampled, but were concentrated at the surface and 4 m.

By using Stokes' law for calculating the rising velocity of the eggs, which have an average diameter of 0.70 mm, we estimated when the eggs were spawned and how old they were when sampled. If eggs were spawned on the bottom (57 m), they required 7 h to rise to 30 m and another 5.8 h to reach 15 m. As several precell and cell stage eggs appeared from 1500 to 1800 h in the 30 m net, the eggs were probably spawned between 0800 and 1100 h. Table 9 is a timetable for development of Gulf Stream flounder eggs based on the stages of eggs in Table 8 and on egg rising velocities calculated from Stokes' law.

The overlap between batches of the Gulf Stream flounder eggs as compared with the clearly defined batches of Atlantic whiting eggs may be related to two factors. First, the incubation time of Gulf Stream flounder is about twice that of Atlantic whiting eggs; therefore, eggs from twice as many batches are present in the plankton at once. Second, because Gulf Stream flounder spawns on the bottom, the eggs were subjected to turbulence and mixing by the time they were

TABLE 9.—Timetable of development of Gulf Stream flounder eggs based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Time	Hours from spawning	Developmental stage	Depth mainly taken (m)
Day 1:			
1500	7	Precell—cell stage	30
1800	10	Precell—cell stage	30
2100	13	Cell stage—early blastula	15
2400	16	Early blastula—blastodermal cap	15
0300	19	Blastodermal cap	15
0600	22	Blastodermal cap	15
0900	25	Early germ ring	4
1200	28	Early germ ring	4
Day 2:			
1500	31	Early germ ring	0-4
1800	34	Migrating germ ring	0-4
2100	37	Migrating germ ring	0-4
2400	40	Early middle	0-4
0300	43	Middle middle	0-4
0600	46	Middle middle	0-4
0900	49	Late middle	0-4
1200	52	Early late	0-4
Day 3:			
1500	55	Tail ⅝ around yolk	0-4
1800	58	Tail ⅝ around yolk	0-4
2100	61	Tail ¾ around yolk	0-4
2400	64	Tail ⅞ around yolk	0-4
0300	67	Tail ⅞ around yolk	0-4
0600	70	Tail ⅞ around yolk	0-4
0900	73	Full circle	0-4
1200+	76+	Hatching	0-4

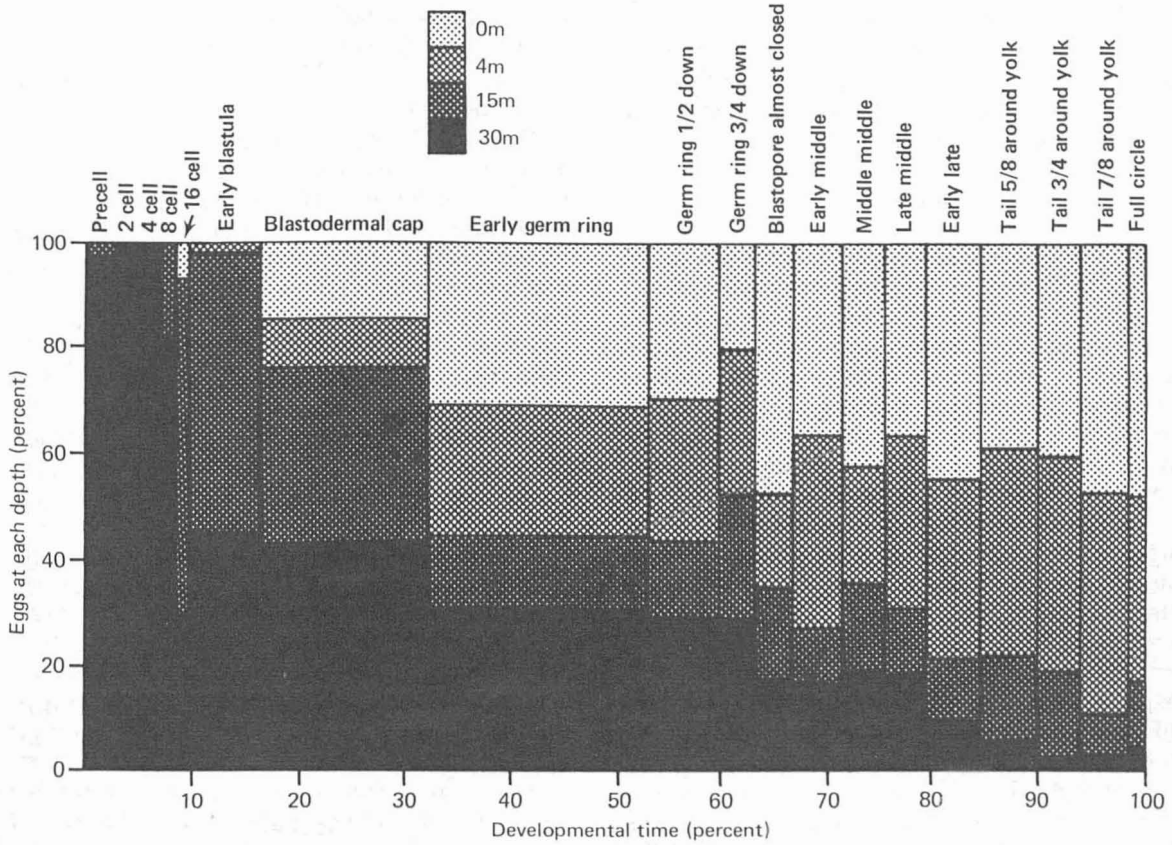

FIGURE 10.—Percentage of Gulf Stream flounder eggs at each depth plotted by age and stage based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

sampled, while Atlantic whiting eggs were collected from depths near where they were spawned.

An overall mean of 124 Gulf Stream flounder larvae/100 m^3 was taken during the cruise (Table 1). More larvae were taken at night than during the day and more were caught at 15 m than at the other depths sampled (Figure 3). The diel-depth interaction was significant in that Gulf Stream flounder, like fourspot flounder, were relatively more abundant at 0 and 4 m at night and at 15 and 30 m during the day, indicating a vertical migration upward at night (Table 2). Gulf Stream flounder larvae are concentrated in the thermocline during the day, but at least some move toward the surface at night.

From the second experiment, it appears that the movement toward the surface may occur in early evening because catches in the 2 m tow were high at 1800 h, while the 15 m tow took more larvae at other times (0000, 0600, and 1200 h). There was no significant difference in catches over the 3 d of the experiment, nor in the mean standard lengths, which ranged from 4.33 to 4.57 mm.

Smaller larvae were taken from 0 to 4 m during the day, while larger larvae were taken from 6 to 30 m (Table 10). At night, it seems that some of the larger larvae spread upward and were caught at

TABLE 10.—Mean standard lengths (millimeters) of Gulf Stream flounder larvae at six depths during day and night from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Depth (m)	Day			Night		
	Mean	SE	No.	Mean	SE	No.
0	3.31	0.267	12	4.10	0.278	114
2	3.55	.285	64	3.82	.370	55
4	4.03	.688	55	4.00	.217	185
6	5.93	2.188	27	4.04	.317	38
15	4.74	.172	328	5.22	.321	135
30	5.69	.414	177	4.40	.128	93

all depths; however, this result may be due to net avoidance by larger larvae near the surface in the daytime. These results are similar to those found for Atlantic whiting, in which larger larvae spread upward to 15 m at night.

Butterfish

An overall mean of 41 eggs/100 m^3 was caught during the cruise, making butterfish eggs third in abundance (Table 1). Fewer eggs were caught at the greatest sampling depths though the eggs at 4 m slightly outnumbered those at the surface (Table 4). In addition, more eggs were taken at night, which could reflect an evening spawning time. No significant differences in the number of eggs taken from day to day was evident.

An overall mean of 50 butterfish larvae/100 m^3 was taken during the cruise. There were no significant differences in numbers of larvae over the 3 d or during day as opposed to night (Table 2), indicating that we were probably sampling a uniform concentration of larvae throughout the experiment. In general, more larvae were taken at 15 m, but the diel-depth interaction indicated that the larvae were more abundant in the 0 and 4 m nets at night than during the day. This pattern is similar to that of Gulf Stream flounder and fourspot flounder indicating that some of the larvae that spend the day in the thermocline move toward the surface at night (Figure 3). The second experiment indicated that the 2 m catches were highest at 1800 h while the 15 m catches were high at all other times.

Fourspot Flounder

Fourspot flounder eggs ranked fourth in abundance, with a mean of 36 eggs/100 m^3 taken during the cruise (Table 1). Fewer eggs were taken at the greatest sampling depths though similar numbers were taken at 0 and 4 m and at 15 and 30 m (Figure 5, Table 4). No significant differences between day and night catches were evident.

An overall mean of 46 fourspot flounder larvae/100 m^3 was taken. The catches were significantly different for all three primary factors, i.e., more were caught at night than in the daytime, more were caught on day 3 than on the first 2 d, and the 15 m tow took more than the other three (Table 2). The interaction between days and depth was significant because on day 2 the surface and 4 m tows had high catches relative to the other days, while on day 3 the 15 and 30 m tows had high catches relative to the other days. Apparently the drogue, which was centered in the upper 10 m of the water column, did not experience the same drift during the experiment as the fourspot flounder larvae, which had their center of abundance in the thermocline at a depth of 15 m. The day-night depth interactions indicated migration by some larvae toward the surface at night since the 0 and 4 m tows had high catches at night while the 15 and 30 m tows had high catches during the day (see Figure 3).

Results of the second experiment show the same pattern in that more larvae were caught at night and the 15 m tow had high catches at all times. However, the 0, 2, 4, and 6 m tows had relatively higher catches at night than during either of the day periods.

These results indicate that fourspot flounder larvae occur mainly in the upper part of the thermocline where temperatures are above 10° C. Those larvae that move from 15 m during the day to near the surface at night, pass from 18° C water to 22° C water. The salinity also changes over this depth range from about 33.6‰ at 14 m to 32.8‰ at the surface.

Hakes

The species of hake (*Urophycis*) eggs and larvae in our samples could not be determined because of overlapping meristic characters and spawning seasons, so more than one species may be represented. An overall mean of 27 eggs/100 m^3 was taken, making hake eggs fifth in abundance. Slightly more eggs were taken at 4 m than at the surface (Figure 5), but otherwise egg numbers decreased with increasing depth (Table 4). No significant differences between day and night catches were evident, indicating that the daily spawning time was prolonged, or that we were possibly sampling more than one species with somewhat different spawning times. Egg concentration in the area of the drogue remained fairly constant. There were no significant differences among the 3 sampling days.

An overall mean of 146 larvae/100 m^3 was taken, making hakes the most abundant larvae caught (Table 1). In general, they were most abundant at 15 m (Table 2), but more were taken in the 0 and 4 m nets at night, and more in the 15 and 30 m nets during the day (Figure 3). During the second experiment, the time-depth interaction

was significant, indicating that during the three time periods examined, the larvae moved to shallower depths at night.

Snake Eel

Snake eel eggs ranked sixth in abundance, with an overall mean of 19 eggs/100 m^3. Fewer eggs were taken in the deeper tows, though slightly more eggs occurred at 4 m than at the surface (Figure 5). No significant difference between day and night egg catches was apparent (Table 4). However, at all depths except 15 m, more eggs usually were taken at night. At 15 m, more eggs were caught in the daytime. Significantly more eggs were caught on each succeeding day of the cruise.

The numbers of eggs in various stages taken during the cruise are shown in Table 11. Because the eggs were not stratified with depth, and because relatively few eggs were taken at each depth, we combined the eggs from the four depths sampled during the first experiment. The eggs are divided into seven batches that were spawned on the 3 d of sampling and the preceding 4 d. Where some ambiguity as to the boundary between older batches exists, replicate samples were staged to provide better definition of individual batches. At each sampling time, four groups of developmental stages were present. Spawning began at 2100 h each day, and was restricted to a relatively short period of time. Most eggs had hatched by 2100 h 4 d after being spawned. These data for development times have been used in a description of embryonic stages in this species (Naplin and Obenchain 1980).

The numbers of eggs in each batch are plotted according to developmental stage and time of day in Figure 11, from which the duration of each stage can be readily determined. For example, complete epiboly required about 12 h and took place from 0900 until 2100 h the day after the eggs were spawned. Table 12 is the corresponding complete developmental timetable for the snake eel. The regular fluctuations in egg number apparent in Figure 11 are even more clearly displayed in Figure 12, which depicts the total number of snake eel eggs over time. The fluctuations occurred on a 12-h cycle, and are possibly the result of tidal periodicity in spawning. As sampling progressed, the vessel gradually drifted into an area of more concentrated spawning, which was somewhat west of and closer to the 30-fathom (54.9 m) line

TABLE 11.—Stages of snake eel eggs taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974. Roman numerals refer to batch numbers that were assigned to the eggs.

Stage	Drogue station:	A	B	C	D	E	F	G	H	I	J	K	L	M	N	O	P	Q	R	S	T	U	V	W	X
	Time:	0600	0900	1200	1500	1800	2100	2400	0300	0600	0900	1200	1500	1800	2100	2400	0300	0600	0900	1200	1500	1800	2100	2400	0300
Precell or unfertilized							2								11								3		
2 cell							5								11								6		
Cell stage								1								2		1						5	
Early blastula							V	2							VI	7	2	19					VII	6	64
Blastodermal cap		16	2						8	12	2	1					14		2						
Early germ ring			32	6	1						45	1						27		2					
Germ ring ½ down	IV			12	3							19	9							14	7	5			
Germ ring ¾ down				1	6	5							15	4							5	5			
Blastopore almost closed						7	3	1					3	20	3							6	8		1
Early and middle closed		7	3			2	21	14	8	11	2	1			30	19	6	11	8	1			15	35	22
Late middle		2	4	1			2		2	11	15			1			3	4	24	10			1		
Early late				6	2	2		1				11					2			7	5				
Tail ⅝ around yolk	III			1	1	1	10	2	4	2	1	2	5	10	10					1	13	16	29	6	3
Tail ¾ around yolk		2	1			1		5		2	5			4	8	10	4		1	1			8	27	14
Tail ⅞ around yolk	II	1							1	7		1					2	12	3	2					2
Full circle				1	2	6	1	1	3	1	1	1	2	2		1		3	3	1	2	2	3	2	6
Tail 1⅛ around yolk		2				3	2			2			2	3	4	2				1	3	2	7	7	3
Tail 1¼ around yolk		1	1			1	1	1	1	2	1				4	2	3				1	1	7	6	12
Tail 1⅜ around yolk	I			1		1			2	2	1					2				3	1	1		1	1
Tail 1½ around yolk						2					1			1											2
Dead					1	1										1			2				2		
Total		30	44	29	16	32	47	28	29	52	74	37	36	45	81	46	36	50	70	43	37	38	87	97	131

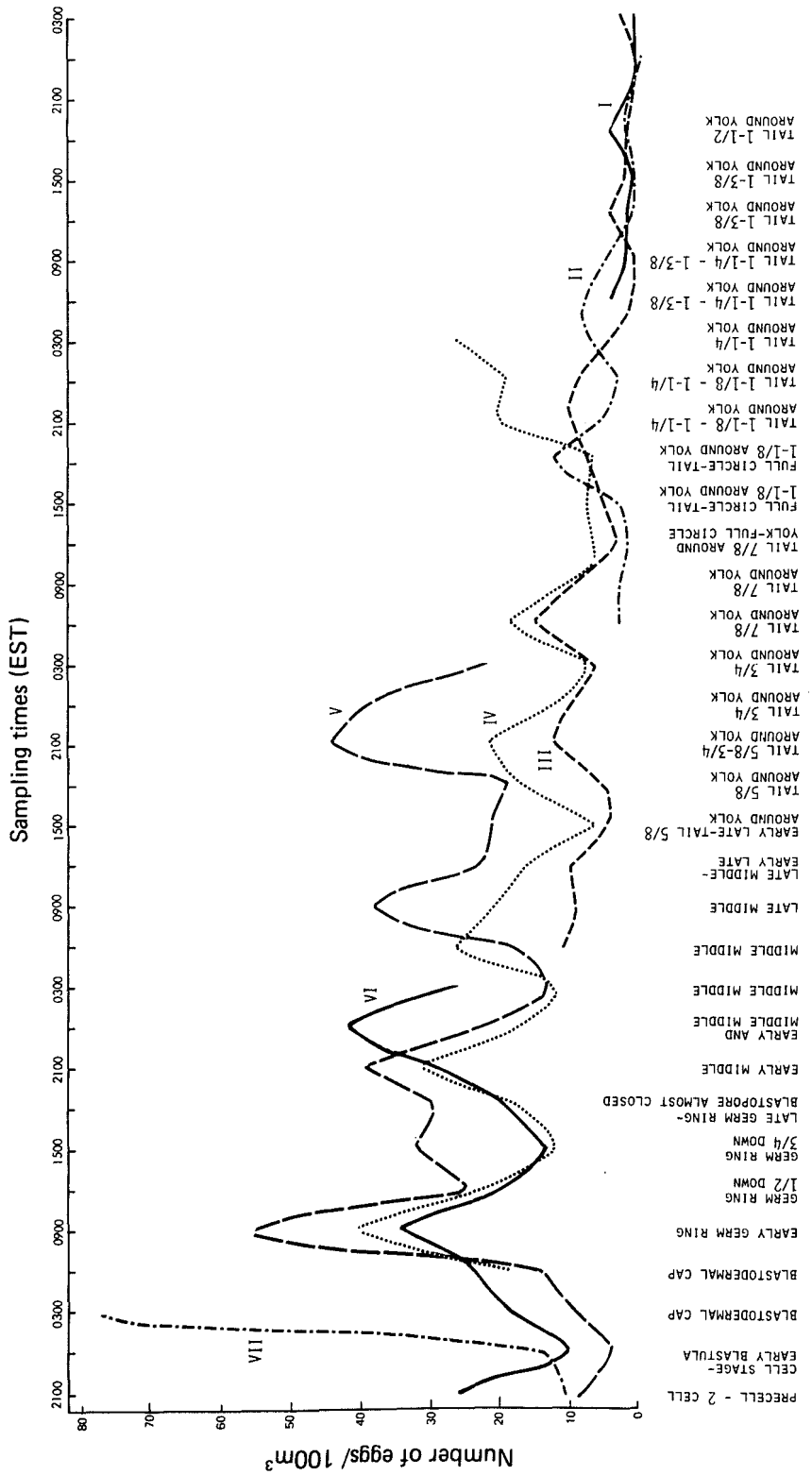

FIGURE 11.—Numbers of snake eel eggs in the seven batches taken during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974, plotted by developmental stage and time of day.

TABLE 12.—Timetable of development of snake eel eggs based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Time	Hours from spawning	Developmental stage
Day 1:		
2100	0	Precell—2 cell
2400	3	Cell stage—early blastula
0300	6	Blastodermal cap
0600	9	Blastodermal cap
0900	12	Early germ ring
1200	15	Germ ring ½ down
1500	18	Germ ring ¾ down
1800	21	Late germ ring—blastopore almost closed
Day 2:		
2100	24	Early middle
2400	27	Early and middle middle
0300	30	Middle middle
0600	33	Middle middle
0900	36	Late middle
1200	39	Late middle—early late
1500	42	Early late—tail ⅝ around yolk
1800	45	Tail ⅝ around yolk
Day 3:		
2100	48	Tail ⅝-¾ around yolk
2400	51	Tail ¾ around yolk
0300	54	Tail ¾ around yolk
0600	57	Tail ⅞ around yolk
0900	60	Tail ⅞ around yolk
1200	63	Tail ⅞ around yolk—full circle
1500	66	Full circle—tail 1⅛ around yolk
1800	69	Full circle—tail 1⅛ around yolk
Day 4:		
2100	72	Tail 1⅛-1¼ around yolk
2400	75	Tail 1⅛-1¼ around yolk
0300	78	Tail 1¼ around yolk
0600	81	Tail 1¼-1⅜ around yolk
0900	84	Tail 1¼-1⅜ around yolk
1200	87	Tail 1⅜ around yolk
1500	90	Tail 1⅜ around yolk
1800	93	Tail 1½ around yolk
2100	96	Hatching

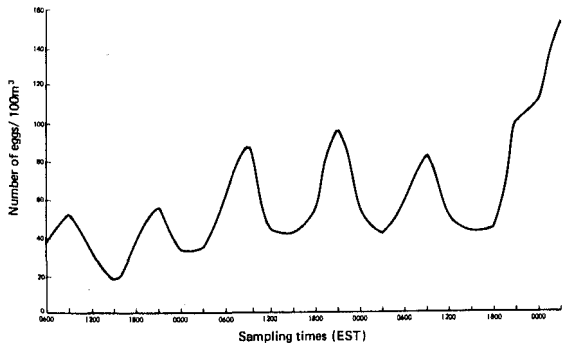

FIGURE 12.—Number of snake eel eggs during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974, plotted by time of day.

than the original sampling site. Because more eggs were taken each day, it was not possible to estimate the total size of any one batch.

A rough estimate of egg mortality within individual batches based on numbers of eggs at different times during their development and at corresponding points of the tidal cycle is approximately 0.5 to 0.6%/h, totaling 48 to 57.6% over the 96 h development time.

Applying Stokes' law to snake eel eggs results in an overall time of only 2.1 h required for eggs to rise from the bottom to the surface. The rapid rising velocity of the eggs is a result of their large diameter ($\bar{X}$ = 2.60 mm). Slightly more time would be required for eggs to rise to the surface if their density is somewhat greater immediately after spawning. In any case, if Stokes' law still holds for eggs of this size, it is inadequate for determining the depth of spawning for snake eel although from behavior of the adults it is likely to occur on or near the bottom.

Few snake eel larvae were caught during the cruise.

Frigate Mackerel

No frigate mackerel eggs were taken during the cruise. Due to nomenclatural confusion, the species of *Auxis* larvae in our collections cannot be determined. However, only one type of larva appears to be represented, and an overall mean of 54 larvae/100 m^3 was caught during the cruise. There were highly significant differences in days, diel, and depth factors (Table 2), indicating that we were not sampling a uniformly distributed population during the experiments. The larvae were more abundant at night than during the day, and more were caught on the second day than on the first or third. Larvae were most abundant overall in the 4 m tow, and more were taken at the surface during day than at night. Catches at 15 and 30 m were so small in both day and night tows that contamination of the nets in shallower water as they passed through the water column could account for them (Figure 3). In the second experiment, the 2 m tow caught most fish at 1800 h, while the 6 m tow caught more at other times. Thus *Auxis* larvae were mostly in the upper 6 m of the water column above the thermocline and were found closer to the surface during the evening.

Smallmouth Flounder

Smallmouth flounder eggs have not been described. Based on the similarity of the early larvae, however, it is likely that they closely resemble Gulf Stream flounder eggs. In view of

the relative proportions of larvae of the two species taken during the cruise, eggs with characteristics of smallmouth flounder and Gulf Stream flounder were assumed to be of the latter species.

An overall mean of 9.1 smallmouth flounder larvae/100 m^3 was taken during the cruise. In general, the 15 m tow caught most of the larvae; however, more larvae were taken at 15 and 30 m in the daytime, while more were caught at 0 and 4 m at night (Figure 3). The larvae moved toward the surface at night and were also more abundant at all depths at night. More larvae were taken on each succeeding day of the experiment (Table 2).

We found little difference in mean length during day tows at all depths, and although the larvae caught at night at 30 m were larger than those caught at other depths, only two were taken (Table 13). The mean lengths of the larvae taken each day remained virtually constant from 3.58 to 3.61 mm. Evidently the drogue gradually drifted into an area of higher larval concentration, resulting in the increasing number of larvae taken each succeeding day.

TABLE 13.—Mean standard lengths (millimeters) of smallmouth flounder larvae at six depths during day and night from the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Depth (m)	Day			Night		
	Mean	SE	No.	Mean	SE	No.
0	—	—	—	3.65	0.102	87
2	3.73	0.515	38	3.41	.410	52
4	4.14	.390	15	3.63	.078	135
6	4.48	.765	8	3.60	.350	40
15	3.42	.098	200	4.06	.298	78
30	4.13	.932	13	5.30	.300	2

DISCUSSION

The two major techniques applied to the egg data, i.e., analyses of variance of egg numbers based on a factorial experimental design and staging the eggs, tend to complement each other. The former technique is used to point out significant variation in the data that may be clarified and elaborated by staging selected egg samples. For example, significant differences in egg number at various times of day revealed by factorial analysis can be accounted for by the daily spawning and hatching cycles revealed by staging the eggs. In our experiments, analysis of variance demonstrated significant changes in egg numbers over four sampling depths, over 3 d, and in the daytime and at night. Egg staging provided us with developmental timetables, and time of day and depth of spawning and hatching. Spawning and developmental characteristics of the three species whose eggs were staged are summarized in Table 14. Atlantic whiting and snake eel eggs were distributed homogeneously by stage over all depths sampled, whereas Gulf Stream flounder eggs were stratified by stage to some extent. Stage stratification of Gulf Stream flounder eggs indicated that spawning probably occurred on the bottom, and rising velocity calculations for these eggs support that conclusion. The rising velocity for Atlantic whiting eggs narrowed the possible spawning depth to the upper 10 m of the water. Fluctuations in egg numbers that appeared to be tide induced could indicate that the bottom-dwelling snake eel spawns on the bottom during a particular time of the tidal current cycle.

In a study of haddock eggs, Walford (1938) found that the eggs were spawned on the bottom and had a tendency to rise. Because egg stages were homogeneously distributed with respect to depth, he concluded that the eggs could adjust their specific gravity within limits to match that of the ambient water. Most planktonic eggs probably possess some capacity to adjust their densities (Walford 1938). However, because a definite age stratification with depth appeared for the Gulf Stream flounder eggs, we can conclude that in this case the eggs rise in the water column more rapidly than they adjust their density to the ambient water.

Spawning and hatching times for the three species were staggered throughout the day, with no two species having similar schedules. Atlantic whiting and snake eel spawned in the afternoon and evening, and while Atlantic whiting eggs hatched in the morning, snake eel eggs hatched at about the same time of day they were spawned.

TABLE 14.—Summary of local characteristics of distribution of spawning and development determined by staging eggs of Atlantic whiting, Gulf Stream flounder, and snake eel, based on collections made during the vertical distribution study of ichthyoplankton in the Middle Atlantic Bight, July 1974.

Characteristic	Atlantic whiting	Gulf Stream flounder	Snake eel
Stage vs. depth	Same stage at all depths	Earliest stages - deepest	Same stage at all depths
Spawning depth	Upper 10 m	Bottom (57 m)	Bottom
Spawning time, h	1500-1800	0800-1100	2100
Hatching time, h	0300-0800	1200-1500	1500-2100
Incubation time	1.5 d (39 h)	3 d (72 h)	4 d (96 h)
No. stages/samples	Usually 2	Usually 3	4

Gulf Stream flounder spawned in the morning and the eggs hatched around noon. The progression from precell to hatching stages in all of these species allowed construction of detailed developmental timetables. Ahlstrom (1943) found spawning to occur during only a few hours of the day, and that plankton samples contained discrete batches of eggs spawned on different days. He also determined developmental times from this information. Ferraro (1980) reported on daily spawning times of a number of species. All fish investigated spawn during limited times of day, mainly at some time between noon and midnight.

For species that spawn on a regular diel basis, the number of predominant stages at any time about equals the number of days the eggs require to hatch (Table 14). Therefore, longer incubation times mean that more days of spawning are represented at any one time, making the separation of eggs into discrete spawning batches more difficult. Atlantic whiting eggs, with a short incubation time and spawned in the upper 10 m of water, were readily separated into discrete batches. Theoretically, snake eel eggs with a development time of 96 h would be more difficult to separate into batches than Gulf Stream flounder eggs with a development time of only 72 h. This was not the case, probably because of the depth stratification of the Gulf Stream flounder eggs and their longer daily spawning period compared with the homogeneous depth distribution of snake eel eggs and their very short daily spawning period.

Among the eight most abundant types of larvae collected during this study, all were more abundant closer to the sea surface at night. Two general patterns were seen: bluefish and frigate mackerel larvae were mostly above the thermocline (most abundant at 6 m) and some migrated to the surface at night; the other six species were most abundant below the thermocline at 15 m during the day but some larvae of each species migrated to waters above the thermocline at night. Within these two patterns, specific variations occurred. No two species showed the same combination of significant F-values for the factors tested and their interactions. We remained in a body of water where factors affecting larval abundance were so constant for three of the species that no significant differences were seen in the catches over the 3-d study. The two species most closely associated with the surface (bluefish and frigate mackerel) showed the greatest fluctuations in abundance over the 3 d, indicating that in following the drogue, we moved to areas where variation in factors affected larval abundance occurred. In such areas where water movement varies considerably with depth, a drogue can be expected to track only uniform patches of those organisms whose depth ranges are similar to that of the drogue. Four species were collected in significantly larger numbers at night than during the day. This may have resulted from increased avoidance by larvae during daylight. However, significantly more Atlantic whiting larvae were taken during day than at night. Some of these differences may thus reflect differences in vertical distribution on a diel cycle. If the larvae were more concentrated during day than at night at one or more of the levels sampled, they would appear more abundant during the day, although their overall abundance in the water column would not actually be different. Significant portions of the larval population of species that were abundant in our deeper nets may have occurred below the depths we sampled.

This study, as have others (e.g., Miller et al. 1963), points out the necessity of sampling the entire water column, at least over continental shelves, during ichthyoplankton surveys. This is accomplished in the many recent surveys which employ oblique or vertical plankton tows. In other sampling designs significant portions of the populations can be either undersampled or oversampled depending on their depth distribution and the time of day of sampling. The implications of this study regarding effects of time of day on numbers of fish eggs in the water column due to diel spawning and embryonic developmental cycles need to be considered in analyzing results of ichthyoplankton surveys.

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