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An Experiment on Factors Affecting Depth Distribution of Larval Herring, *Clupea harengus*, in Coastal Maine

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Abstract

The vertical distribution of larval herring, *Clupea harengus*, in Sheepscot Bay, Maine, in the spring of 1967 was examined in relation to three factors: incident light, tidal phase, and depth of sampling. The results of a factorial analysis indicated that catches were significantly greater than average in deep tows on bright days and in shallow tows on dull days. This interaction accounted for about 36% of the variability. The experiment therefore indicates a potential bias in the results from the annual spring surveys of larval herring abundance in coastal Maine waters based on sampling only the shallow (0-20 m) portion of the water column. The methodology employed in this study could be helpful to those investigating, with limited resources, estuarine and coastal distributions of organisms, and to those seeking to investigate some of the contradictory evidence relevant to depth distribution of herring larvae.

Introduction

The fishery for juvenile herring in coastal waters of Maine harvests mainly two age-groups (2- and 3-year-old fish), and catches are therefore especially sensitive to fluctuations in recruitment. An unusually severe fluctuation occurred in the early 1960's, when 113,000 tons (metric) were taken in 1960 and only 23,000 tons in 1961. In an effort to anticipate such fluctuations for the fishing industry, larval herring were sampled along the Maine coast to determine if indices of larval abundance or their correlates could be used to forecast yields.

Results from a series of coastal surveys in 1961-66 indicated that the average catch rate of herring larvae during the spring was a potential abundance index, but the rocky coastal waters caused sampling difficulties. To avoid the numerous submerged rock ledges, tows were made only in areas of relatively deep water where sampling was possible to a maximum depth of 20 m, thus perhaps causing a bias in the resulting estimates of larval abundance. Graham *et al.* (1972) found that the coastal circulation transported the larvae during their shoreward migration during the spring and that the circulation was controlled partially by bottom topography (Graham, 1970a). Presumably, the preliminary coastal surveys sampled larvae from only a certain portion of the transporting circulation. To avoid possible bias in the results of subsequent surveys, a stratified-random sampling scheme was implemented in the spring of 1967, based on division of the surveyed area into 10′ x 10′ rectangles of latitude and longitude, in each of which two tows were made to a maximum depth of 20 m and their catches averaged.

Concurrent with the implementation of the sampling scheme, a special study of the depth distribution of larval herring was carried out in the spring of 1967 to determine the possible effects of depth on mean catch rates from daylight surveys. This paper presents the results of that study and discusses the possible effects of depth limitation of sampling on larval herring migration and on the spring survey data. An explanation for the contradictory results often obtained in studies on the depth distribution of larval herring is also suggested.

Methods

Sampling design

An experiment was designed to permit sampling during the relatively few days when ship-time and personnel were available. The design was a 2^3 factorial analysis (Graham, 1972a) which examined three factors that might affect the depth distribution of larval herring: light intensity, tidal phase, and depth of sampling. Incident light was chosen for study because of its possible influence on depth distribution (Blaxter, 1973). Tidal phase was chosen because it affects the vertical distribution and migration of larval herring in the Sheepscot River estuary (Graham, 1972a). The levels selected for the factors were: dull and bright days, ebb and flood tidal phases, and shallow and deep tows.

Incident light was measured with a deck cell of an irradiance meter having a Wratten No. 2 filter, which adjusted the response of the cell to match that of the human eye. Incident light on the bright day varied from

45,161 to 64,516 lux (4,200–6,000 foot-candles) and on the two dull days from 13,978 to 20,430 lux (1,300–1,900 foot-candles). The bright day was largely cloudless, whereas the dull days were heavily overcast with intermittant rain. The sampling was carried out on 14 April, 24 April and 3 May. Secchi disc readings taken during approximately the same period in previous years indicated relatively small variation in light extinction with water depth, the recorded depths in mid and late April being 7 and 7.75 m respectively in 1962, 3 and 4 m in 1963, and 3 and 5 m in 1965.

Tidal phase was judged by the direction of the surface current which paralleled the long axis of Sheepscot Bay. Sampling was delayed until the current was well developed to avoid any possible lingering flow of the opposite tidal phase near the bottom. Subsequent investigation of currents in the vicinity of the sampling station indicated that this was a reasonable procedure (Graham and Morgan, 1976).

All tows were made with a Boothbay Depresser trawl No. 4 at the same location in the mouth of the Sheepscot River estuary, Sheepscot Bay, Maine, where the water depth was about 60 m. Shallow tows were those from just below the surface to 20 m and deep tows were those from 30 to 50 m. On 14 April (a bright day) two shallow tows and two deep tows were made at 4 knots (2.06 m/sec) during the ebb tide and four similar tows were made on the subsequent flood tide. Four similar tows were made during an ebb tide on 24 April (a dull day) and again during a flood tide on 3 May (a dull day).

Each tow was a stepped oblique haul, deep tows having steps at 50, 40 and 30 m and shallow tows with steps at 20, 10 and 1.5 m below the surface. Previously calibrated, the amount of towing wire deployed indicated the depth reached by the trawl. Towing trials with Boothbay Depresser trawls indicated that they were stable underway (Graham and Vaughn, 1966), and calibrations showed that the ratio of towing wire deployed to depth of trawl was 3.1:1. Upon completion of a deep tow, the trawl was winched to the surface at approximately 1 knot (0.51 m/sec). Considering the large size of herring larvae in the spring and their ability to avoid the trawl (Graham *et al.*, 1972), it is unlikely that larvae would be captured in the upper water during this slow retrieval. There were no closing devices adaptable to the trawl when this study was carried out in 1967.

Each tow was timed to last 7.5 minutes with 2 minutes at each step. This short tow duration permitted the completion of each series of four tows within 1 hour, as a longer period might have allowed the transportation of larval concentrations out of the sampling area by the tidal flow. A series of current measurements made later in the vicinity of the towing location indicated that currents sometimes exceeded 50 cm/sec. (Graham and Morgan, 1976), implying that a group of larvae could be transported approximately 1.8 km in an hour. All tows were made in the direction of the current flow. The trawl strained water efficiently (Graham, 1972b), and, when calibrated for a known distance towed during 7.5 minutes, it strained 1,343 m^3 of water through the 1.45 m^2 mouth opening and the 3-mm mesh openings of the liner which was tied at the end.

Mesh opening

The 3 mm mesh size of the liner was larger than the standard mesh size (2 mm) used during the spring surveys, and larvae less than 37 mm (standard length), with average body depth of 3 mm, could be expected to pass through the meshes of the liner. However, earlier studies had shown that larvae with body depth less than the mesh opening are retained by the trawl liner.

In one study, a Gulf III sampler (Gehringer and Aron, 1968) and a Boothbay Depressor trawl No. 1 were towed at each of 21 stations along the Maine coast. The open-mesh diameter of the Gulf III was 0.366 mmm and that of the trawl was 4 mm. One gear was towed towards a given station and the other away from it. Tows at 4 knots (2.06 m/sec) were 30 minutes duration with 10-minute steps at 20 and 10 m and at the surface. The Gulf III captured larvae of two modal lengths (12 and 18 mm), whereas the trawl captured only the larger-sized larvae (Fig. 1A). The largest larva captured was 33 mm, which corresponds to an average body depth of 2.5 mm. The capture of larvae of this size and smaller demonstrates that the trawl will retain larvae with body depths less than the mesh opening of the liner.

In another study, conducted by the Boothbay Harbor Laboratory, two boats, one with a Boothbay No. 1 trawl (4-mm mesh liner) and the other with a larger Boothbay No. 4 trawl (2-mm mesh liner), towed simultaneously towards and past each other through a narrow channel (0.5 km wide) of the Sheepscot River estuary. Tows lasted 10 minutes at towing speeds of 4 knots (2.05 m/sec) for the No. 1 trawl with mouth opening of 1 m^2 and 4.5 knots (2.32 m/sec) for the No. 4 trawl with mouth opening of 4.2 m^2. Effort (m^3) was determined from calibrated flow-meters mounted in each trawl. The size ranges of larvae (two samples from horizontal tows near the surface and two at 10 m for each trawl) and the average catch rates were similar (Fig. 1B), although there was a slight difference in modal lengths. Apparently, the retention of larvae with smaller body depth than the liner mesh openings is caused by the peristaltic action of the trawl nets (Graham, 1972b).

For the 1967 experiment described in this paper, it was assumed that gear selectivity was constant during all tows and that changes in the size composition of the

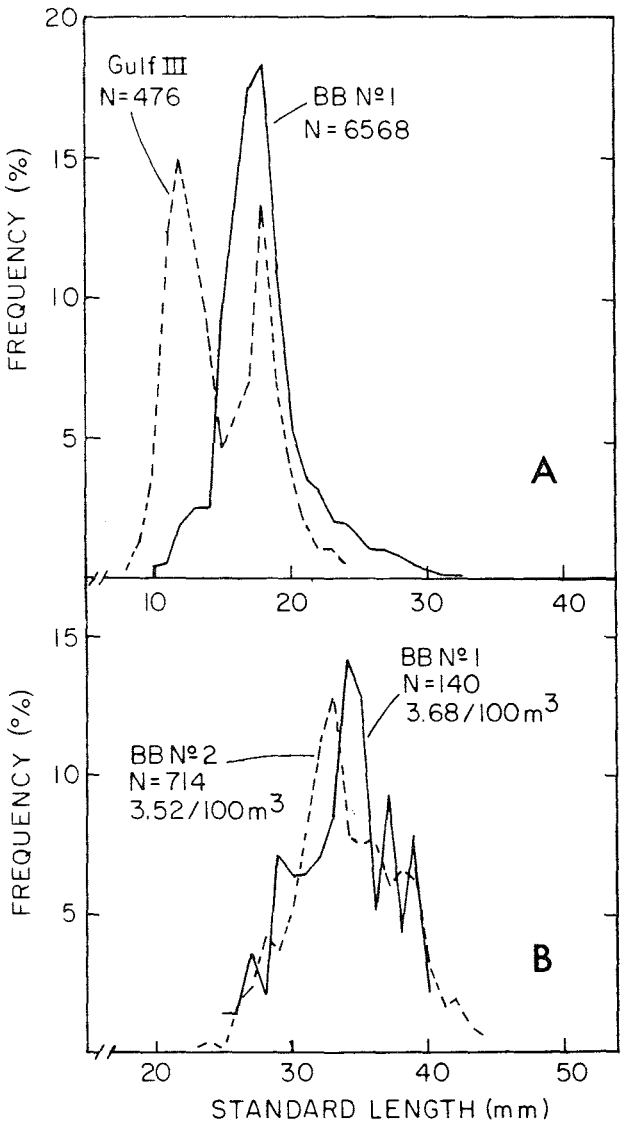

Fig. 1. **A**, length distributions of larval herring captured in the Gulf III sampler (mesh size 0.366 mm) and a Boothbay Depressor trawl No. 1 (mesh opening 4 mm). **B**, length distributions of larval herring and average catch rate for 4 tows with Boothbay Depressor trawls No. 1 and 2 with mesh openings of 4 mm and and 2 mm respectively.

population sampled were not so large as to invalidate the measures of larval density.

Results

Catch and size of larvae

During the 1967 spring experiment, the 16 tows captured 1,028 herring larvae, with individual catches varying from 11 to 208 larvae (Table 1). The overall length composition of all samples had a range of 24-42 mm with the mode at 33 mm (Fig. 2). Larvae taken on the three different sampling dates exhibited different length frequency distributions, with modal lengths at 34-35 mm, 33 mm and 37 mm for the larvae taken on 14 April, 24 April and 3 May respectively.

TABLE 1. Replicate catches of larval herring for two levels of daylight, tidal phase and tow depth in the Sheepscot estuary experiment, 1967.

Day	Tide	Shallow tows (0-20 m)		Deep tows (30-50 m)	
		(1)	(2)	(1)	(2)
Dull	Ebb	208	197	49	11
	Flood	51	72	21	21
Bright	Ebb	13	51	109	51
	Flood	40	64	35	35

The sharp decline in the frequency of large larvae (⩾40 mm) on May 3 probably reflects larval avoidance of the gear and their unavailability. Comparison of night *versus* day trawl samples by Graham *et al.* (1972) indicated that avoidance by larvae began when they were 37 mm long and was appreciable when they reached 40 mm. They also found that the larvae assumed a juvenile form at about 45 mm in length and schooled in shallow water of coves and bays usually in late April.

Statistical analysis

Analysis of variance of the transformed experimental data ($\log_{10}$) indicated that the interaction of daylight and depth was significant at the probability level of $P = 0.05$ and accounted for approximately 36% of the total variability (Table 2). The catch rates of larvae were greater than average for deep tows on bright days and for shallow tows on dull days. Plots of the residual errors were examined to determine if uncontrolled factors influenced the results. There was no evidence of a trend in the frequency plot of residuals or in their comparison with sampling order. The possible influence of larval size on the results in Table 2 was examined by a stepwise regression with mean larval length, light, tide, depth, all possible first-order interactions, and the light-tide-depth interaction as independent variables and the common logarithms of the larval catch rates as the dependent variable. Neither length nor any of the length interaction terms produced statistically significant reductions in the residual sums of squares. Evidently, length of larvae had not confounded the experimental results.

Discussion

The results of studies on the vertical distribution of larval herring are often contradictory. Reviews of past literature by Seliverstov (1974) and Lough (MS 1975), concerning day-night comparisons of larval catches as evidence of diurnal migration, revealed that some researchers reported large catches by day and others reported large catches by night. Regarding larval size, the larger larvae were reported, in some cases, to be more abundant either near the surface or near the bottom during the day; in other instances, the larger larvae were more abundant near the surface at night.

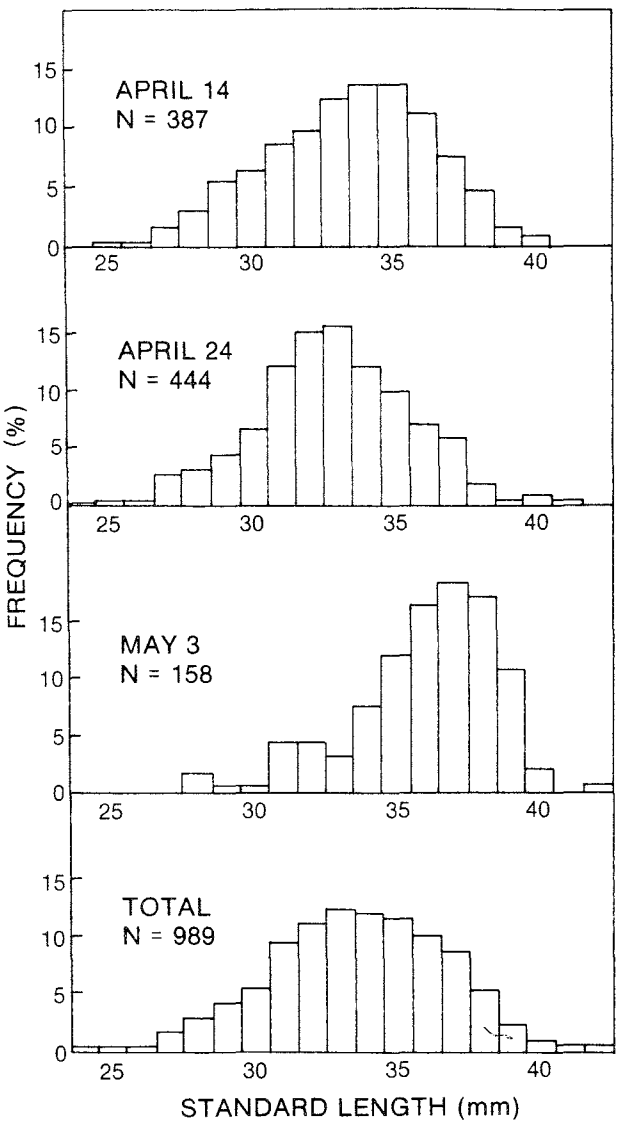

Fig. 2. Length distributions of larval herring captured with a Boothbay Depressor trawl No. 4 (mesh opening 3 mm) during the Sheepscot Bay experiment in the spring of 1967.

Recent research has further revealed the considerable variability exhibited by the vertical distribution of larval herring. Sjoblom and Parmanne (1978) found that larval herring in the Gulf of Finland were in relatively deep water by day and closer to the surface at night during the early summer, but that these positions were reversed later in the summer. They could not explain this behavior by either the amount of light present or the size of larvae, although vertical migration was more pronounced for large larvae. The vertical migration of the larvae was not associated with water temperature, vertical temperature gradient, wind velocity or vertical distribution of zooplankton. Grainger (1980) observed that the abundance of larval herring (7–12 mm long) in Galway Bay, Ireland, was high during daytime at or near the surface and

TABLE 2. Analysis of variance of larval herring catches for the three factors considered in the Sheepscot estuary experiment, 1967.

Factor	Sum of squares	df	Mean square	F ratio
(A) Daylight	0.0151	1	0.0151	0.26
(B) Tidal phase	0.0908	1	0.0908	1.53
(C) Tow depth	0.3020	1	0.3020	5.20
(A) (B)	0.0708	1	0.0708	1.20
(A) (C)	0.7245	1	0.7245	12.24[a]
(B) (C)	0.0050	1	0.0050	0.08
(A) (B) (C)	0.3036	1	0.3036	5.13
Within	0.4733	8	0.0592	
Total	1.9851			

[a]Statistically significant; $P_{0.05} = 5.32$, $P_{0.01} = 11.26$.

decreased with depth. There was no significant variation in larval length with depth, and the factors affecting light intensity in the water were not associated with the mean depth of the larvae. Dubravin *et al.* (1976), in studying the vertical distribution of larval herring in the North Sea, found that 6–12 mm larvae were most abundant under the continuity layer, whereas 13–21 mm larvae performed two vertical migrations daily, returning to the discontinuity layer after sunset and after sunrise. Potter and Lough (MS 1980) studied the vertical distribution of herring larvae on Nantucket Shoals, off northeastern United States, sampling the same concentration of larvae over a period of 10 days. On the first day of sampling, larvae were most abundant in the surface layer during both day and night, but, on the second day, larvae were distributed uniformly throughout the water column during day and night. The length range of larvae was 5–30 mm, and there was a gradual increase in size with depth. Lough (MS 1975) suggested that perhaps generalizations concerning the vertical distribution of larval herring cannot be made for different water masses because behavior differs with changes in environmental conditions. He also noted that larval reactions to light may vary with development stage, as indicated by the research of Seliverstov (1974).

A laboratory study by Wales (1975) indicated that larval herring reactions to light are very complex. His experiments with blinded larvae showed that response to light intensity could be divided into phototaxis and extraretinally evoked kinesis, which could not be separated in sighted larvae. If their response to light intensity in the water column is phototaxic or extraretinal or both, it will be difficult to determine cause-effect relations from field studies.

In many field studies of the vertical distribution of larval herring, researchers have collected larvae from seemingly single populations and have simultaneously conducted extensive environmental monitoring.

Grainger (1980) used multiple regression techniques to examine the relationships between larval behavior and environmental factors. Saila (1964) suggested that the initial data-gathering should be considered exploratory and be used for the preliminary screening of environmental variables, and that subsequent studies should use factorial designs as a potential technique for examining larval responses to environmental factors. Field studies, which monitor larval behavior and environmental factors without the assurance of sampling wide ranges and diverse combinations of environmental conditions, might expend considerable effort and not discern which factors and interactions affect larval behavior.

Although the results cannot be considered conclusive, the Sheepscot Bay experiment was an unusual larval herring study, because the sampling design required little effort but yet enabled the examination of a wide range of some environmental factors and their interactions (Tables 1 and 2). However, it did not indicate how larval herring responds to intermediate light conditions in the area. The response could be continuous or discontinuous. A continuous response to changes in light intensity implies that a complex array of circumstances would be needed to move the larvae to those depths which enable their transport shoreward each spring. A discontinuous threshold response at extreme conditions, however, would permit the larvae to adapt to the "best depths" during intermediate conditions. The nature of this behavioral response might be responsible for some of the apparent contradictions in the literature concerning the influence of light on the depth distribution of larval herring.

The results of the Sheepscot Bay experiment indicate that the estimates of larval abundance derived from spring coastal surveys were biased by restricting the daytime sampling depth to a maximum of 20 m. The significant light-depth interaction indicates that shallow samples taken on a dull spring day would overestimate the true average density at a station, and, conversely, shallow samples taken on a bright day would underestimate the true average density. Despite this problem, the same survey design was continued, because natural variation in light intensity (Graham, 1970b) during the course of a survey was assumed to mitigate any systematic effects on the mean catch rates. To extend the depth range of sampling would require that certain coastal areas be excluded from the cruise tracks because of highly irregular bottom topography. The magnitude of systematic errors that would be created by sampling only selected portions of the water masses which transport the larvae was considered to be greater than that caused by sampling the whole area to a depth of only 20 m.

The results of the 1967 experiment indicated the need for further investigation into the effects of light and other factors on the vertical distributions of herring larvae in Sheepscot Bay. Hydrographic studies, including currents, were conducted in the bay during the summer of 1973 and the study of currents was repeated in 1974 (Graham and Morgan, 1976). Exploratory nighttime sets of buoyed and anchored nets were made in the center of the bay, daytime trawl tows were made along the sides of the bay, and experimental survey designs were formulated. However, the low level and increased variability of larval herring abundance during the 1970's (Graham, MS 1980) prevented the successful completion of the project.

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