RETENTION OF LARVAL HERRING WITHIN THE SHEEPSCOT ESTUARY OF MAINE

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ABSTRACT

This paper demonstrates a system of larval movements that retains larval herring within an estuary despite its seaward residual flow. Data are reviewed from a 2^3 factorial design using buoyed and anchored nets in a narrow channel of the estuary. Three factors were involved: location, tidal phase, and depth. Catch rates of larvae relative to these factors suggested that the larvae maintained their position in the upper portion of the estuary by (1) occupying the landward net tidal flow near the bottom, (2) moving upward upon reaching the limit of their landward penetration (3) then seaward in the net flow near the surface, and (4) finally descending again into the landward net flow.

Larval herring, *Clupea harengus harengus* Linnaeus, move up the Sheepscot estuary of Maine primarily in the autumn and spring. During these seasons the larvae accumulate in the upper portion of the lower estuary where they are retained despite the residual seaward flow of the estuary. Statistically significant differences in the distribution of larval herring according to depth and location and the interaction of these two factors with tide suggested that the larvae were using tidal flows to migrate (Graham and Davis, 1971). This paper examines the data, upon which the statistical results were based, to demonstrate a system of larval movements that retain the larvae within the estuary.

MATERIALS AND METHODS

Buoyed and anchored nets were fished (Figure 1); their construction and validity in sampling larval herring is noted briefly in this paper and is available in detail in another paper (Graham and Venno 1968). Four nets were attached to one line which was buoyed at the surface and anchored to the bottom to sample at predetermined depths (0, 10, 15, and 20 m). A flow meter measured the amount of water strained, from its central position in the mouth of each net. The mouth opening of the net was 0.5 m in diameter and the length of the net was 1.9 m. Mesh diameter was 0.75 mm. Filtration efficiencies of the net ranged from 80 to 90% at current speeds above 15 cm/sec and 100% within speeds from 15 to 3 cm/sec. Below 3 cm/sec the impeller of the flow meter does not revolve. Tests simulating sampling conditions showed that clogging did not change these filtration efficiencies.

The nets fished approximately 6 hr on the flood and 6 hr on the semidiurnal ebb tides. They were set at slack water during dusk, retrieved and reset at the end of the tidal stage during slack water. Two lines of nets were set at the landward end of the estuarine channel and two were set at the seaward end (Figure 2). The sampling area within the estuarine channel was 9 km long, 275 m wide, and about 20 m deep throughout its length. The distance between sets at the seaward end of the channel was 2 km, that between the landward sets was 3.2 km, and the distance between the two locations was 3.8 km as measured from the interior sets.

For a given line of nets catch rates were determined for the two nets above mid-depth and for the two nets below mid-depth. In each case, the total amount of water strained for the two nets above and below mid-depth was

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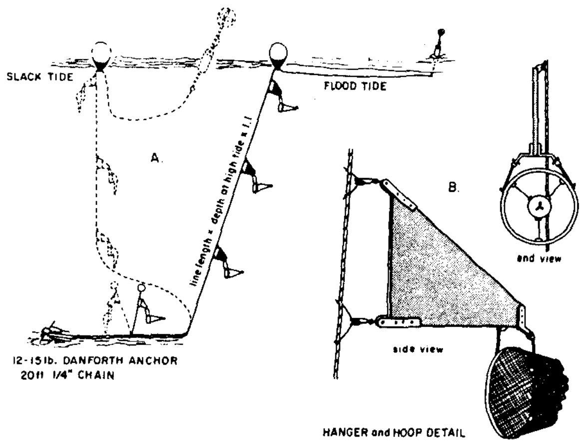

FIGURE 1.—Buoyed nets for sampling larval herring. A, positions of four nets during slack and flowing tides; B, arrangement of hanger and hoop (After Graham and Venno, 1968).

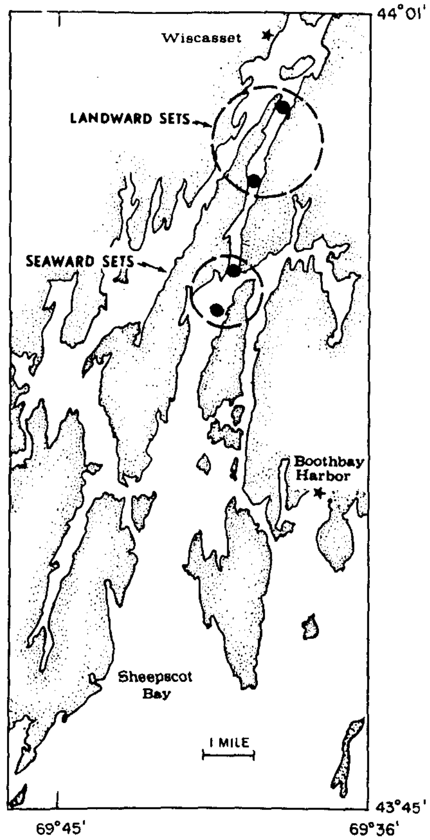

FIGURE 2.—Locations (circled) of buoyed and anchored nets in the Sheepscot estuary of Maine (after Graham and Davis, 1971).

divided into the total number of larvae captured and multiplied by 100 to obtain catches per 100 m^3. Thus, at each location (landward and seaward) average catch rates from the two lines of nets were obtained for two depths (shallow and deep) during two tidal stages (flood and ebb), providing eight samples for each location or 16 samples for a single overnight experiment.

The nets were fished during darkness because the larvae avoided the nets during daylight. A comparison of nighttime catches between two lines of buoyed nets set in tandem within the channel and a comparison between nighttime catches of buoyed nets with those of a high speed Boothbay Depressor Trawl (Graham, Chenoweth, and Davis, 1972) suggested that the larvae did not avoid the net at night nor did they escape from the nets during slack water. The average catches above and below mid-depth determined the concentration of larvae in the water layers above and below the level of no-net-motion of the tidal flows. Larvae in the upper layer would experience a net seaward transport and those in the lower layer would experience a net landward transport. In addition to sampling larvae already in the channel, the two lines of nets in the landward location would sample larvae transported into the channel by the ebb tide and the two lines in the seaward location would sample larvae transported into the channel by the flood tide.

The arrangement of the nets and catches in the estuarine channel constituted a factorial sampling design. A factorial design is especially adaptable to examining the effects of a number of different factors which vary in a regular way during an experiment. The source of regularity in the experiments was the tidal currents transporting the larvae. An example of the statistical procedures is given in Table 1. Catch rates were transformed into common logarithms to obtain a normal distribution of the data for computations. In this paper the untransformed catch

TABLE 1.—Statistical procedures for a 2^3 factorial design using larval catches per 100 m^3 of water strained from an experiment during Nov. 8, 1967. I) Factors are coded, II) Catches are assigned to the factorial order, III) the sums of squares are determined, IV) they are applied to an analysis of variance, and V) a conclusion is determined from the analysis.

I. *Factors and their codes (A).*

Tidal phase	(A)	flood	(+)	ebb	(−)
Water depth	(B)	shallow	(+)	deep	(−)
Location	(C)	landward	(+)	seaward	(−)

II. *Factorial order (1) of larval catches per 100 m^3.*

		Seaward location		Landward location	
Flood	Shallow	5.44(4)	9.78(4)	2.64(8)	5.54(8)
	Deep	11.53(2)	3.51(2)	86.09(6)	48.60(6)
		Seaward location		Landward location	
Ebb	Shallow	2.89(3)	6.29(3)	33.28(7)	24.73(7)
	Deep	0.44(1)	4.73(1)	26.75(5)	4.58(5)

III. *Determination of the sums of squares for the 2^3 factorial design using logarithms of the catches; 1 has been added to each characteristic.*

Factorial order			A	B	AB	C	AC	BC	ABC
(1)	0.6435	1.6749	−	−	+	−	+	+	−
(2)	2.0618	1.5453	+	−	−	−	−	+	+
(3)	1.4609	1.7987	−	+	−	−	+	−	+
(4)	1.7356	1.9903	+	+	+	−	−	−	−
(5)	2.4273	1.6609	−	−	+	+	−	−	+
(6)	2.9350	2.6866	+	−	−	+	+	−	−
(7)	2.5221	2.3932	−	+	−	+	−	+	−
(8)	1.4216	1.7435	+	+	+	+	+	+	+
		Total =	+1.5382	−0.5694	−4.1060	+4.8792	−1.9718	−2.6984	−2.4612
Sums of squares		(Total) $^2/_{16}$ =	0.1479	0.0203	1.0537	1.4879	0.2430	0.4521	0.3786

IV. *Analysis of variance.*

Factor	Sum of squares	Degrees of freedom	Variance	F-ratio
A	0.1479	1	0.1479	1.04
B	0.0203	1	0.0203	0.14
AB	1.0537	1	1.0537	7.40*
C	1.4879	1	1.4879	10.45*
AC	0.2430	1	0.2430	1.71
BC	0.4521	1	0.4521	3.17
ABC	0.3786	1	0.3786	2.66
Within	1.1394	8	0.1424	
Total	4.9229	15		

*Statistically significant, $P_{.05}$ = 5.32

V. *Conclusion.*

Significantly more larvae were captured below mid-depth (deep) on the flood tide and more above mid-depth (shallow) on the ebb tide. In addition, significantly more larvae occurred at the landward location than at the seaward location.

rates are used because they are more familiar than logarithms as measures of concentrations of larval fishes in their environment. The results of the statistical analysis are given by Graham and Davis (1971). Significant differences between catch rates with depth and location and the interaction of these two factors with tide occurred primarily in the autumn and spring. Of eight experiments conducted from late October to early December (1965-67) five had significant differences between larval catch rates. Of 10 experiments completed between mid-March and mid-May (1966-68) six had significant differences between catch rates. The distributions of larvae from experiments that had significant differences in larval catch rates will be described, and an explanation for the absence of significance in the other experiments will be discussed.

RESULTS AND DISCUSSION

Concentrations of larval herring were evident within the channel when the distributions of catch rates that differed statistically within the experiments were examined. The analysis of variance from an experiment on November 8, 1967 (Table 1, IV) showed that the catch rates of larvae differed significantly with location and with the interaction of depth and tide. The untransformed catch rates showed that concentrations of larvae were shallow during the ebb tide and deep during the flood tide. Also, more larvae occurred at the landward end of the channel than at the seaward end. These data and those from other experiments having significantly different distributions in catch were summarized in Table 2. For example, the interaction on November 8 was illustrated by first summing all of the cubic meters of water strained by the shallow nets and then all of the larvae captured by them. These totals were used to obtain an average catch per 100 m^3 of water strained; the process was repeated for the deep nets. Beginning anew, the average catch rates were determined for the two locations. The numbers in parentheses in Table 2 locate the concentrations of larvae within the channel diagrammed in Figure 3. Those concentrations of larvae captured in the shallow nets had a net transport seaward during an experiment and those in the deep nets were transported landward. A transition in such transport occurred for those larvae concentrated throughout the water column at one location or the other. The arrows in Figure 3 infer a system of movements from the location and transport of the larvae that appears analogous to those of other larval fishes (Pearcy and Richards, 1962) and planktonic organisms (Bousfield, 1955) which are retained in estuaries by tidal currents. The suggested movements

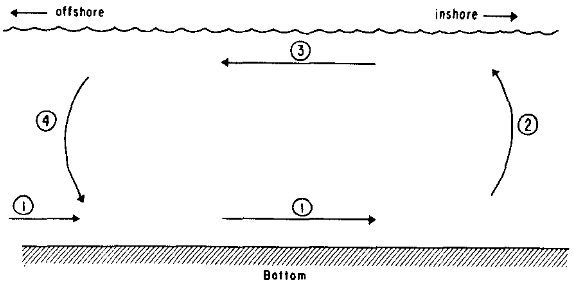

FIGURE 3.—Diagram of a system of larval movements thought to retain larval herring in the Sheepscot estuary. The numbered distributional components of the system coincide with the numbered catches in Table 2.

TABLE 2.—Catch rates from 11 experiments in the autumn and spring. The distributions of rates for single factors and for two factors (interaction X) are given. Numbers in parentheses are from Figure 3; unnumbered catch rates are discussed in the text.

Single factor—depth

	Dec. 7, 1967	*Mar. 20, 1967*	*May 4, 1967*
Shallow	1.95(3)	0.62	40.64(3)
Deep	0.60	7.15(1)	7.66

Single factor—location

	Nov. 8, 1967	*Nov. 21, 1966*	*Dec. 7, 1967*	*Mar. 14, 1968*
Landward	29.56(2)	20.76(2)	1.84(2)	6.16(2)
Seaward	6.60	11.43	1.26	2.06

Two factor—depth × tide

	Flood	*Ebb*	*Flood*	*Ebb*	*Flood*	*Ebb*
	Nov. 1, 1965		*Nov. 8, 1967*		*Nov. 21, 1966*	
Shallow	4.20	11.12(3)	6.11	18.57(3)	3.84	15.46(3)
Deep	10.40(1)	1.43	48.42(1)	18.17	34.85(1)	8.96
	Dec. 6, 1966		*Apr. 27, 1966*		*May 9, 1967*	
Shallow	10.08	4.03	16.74	14.53	18.80	4.40
Deep	1.48	7.94	8.74	20.84	2.78	12.10

Two factor—location × tide

	Flood	*Ebb*	*Flood*	*Ebb*
	Mar. 26, 1966		*Apr. 26, 1966*	
Landward	3.41	11.46(2)	16.98	15.28
Seaward	10.54(4)	1.66	9.32	27.27

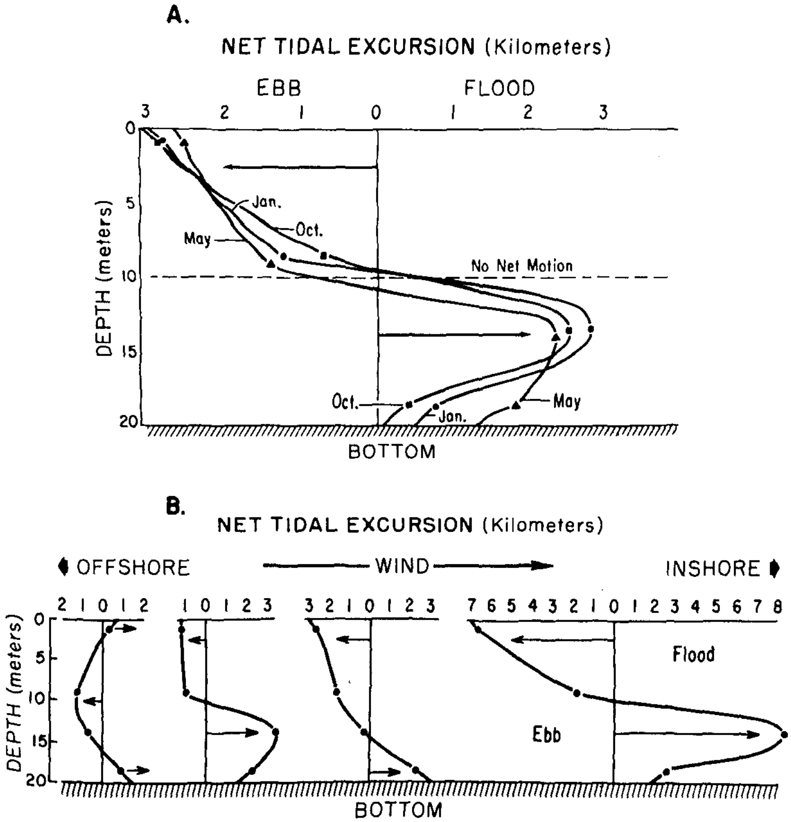

FIGURE 4.—A. Vertical profiles of mean tidal excursion for the four sets of buoyed nets in the estuary of the Sheepscot River (after Graham and Davis, 1971). B. An effect of onshore wind on the net tidal excursions for individual sets of nets in the estuary.

would retain the larvae within the channel after they had entered it on the net flood tide near the bottom.

The system of movements diagrammed in Figure 3 is based on the average two-layer semidiurnal tidal flow (Figure 4A). But the dynamics of estuarine flow can be changed by large amounts of freshwater discharge, wind direction and velocity, and the shape of the channel. Graham and Venno (1968) found that an increase in freshwater discharge and the shape of the channel could change considerably the catch of buoyed nets in the Sheepscot estuary. Although the nets were positioned in the experimental design to lessen such effects, three of the experiments had results that could not be attributed to the system of movements; they are unnumbered in Table 2. All three had interactions between depth and tide and in one case (April 27, 1966) between location and tide as well. The distribution of larval catches was opposite to that expected. For instance, catch rates were larger on the flood tide near the surface and on the ebb tide near the bottom. Because tide was involved in each case possibly these data resulted from unusual tidal dynamics. On May 9, 1967, tidal excursions were modified by winds. Winds blew landward and up the channel during the day preceding the setting of the nets and continued through the flood tide on the night the nets were set. Wind velocities were usually 10 to 20 knots with gusts up to 30 knots. Readings from flow meters showed a typically shaped profile of net tidal excursion at the most landward station (Figure 4B). This was progressively altered seaward until the last station had a small net upstream flow at the surface. Apparently, the winds reversed the tidal flow to some extent and thus the larval distribution as well.

Although I cannot account with certainty for the system of larval movements in the sampling area, the most reasonable explanation is that the larvae responded to changes in the character of the tidal flow. Larvae are transported up the estuary at about 1.8 knots per semidiurnal tidal cycle (Graham and Davis, 1971) which approaches the average length of tidal excursions recorded at 15 m, below the level of no-net-motion. This level of no-net-motion is obliterated in the upper estuary where the maximum depth is 10 m and the channel widens and extensive mud flats are present. The transition zone between the lower and upper estuaries is near the town of Wiscasset (Figure 2) and coincides with the maximum shoreward penetration of an abundance of larvae. Stickney (1959) states that the upper estuary compared to the lower has a greater exchange ratio, lower and more variable salinity and a wider range in temperature. A reversing tidal falls 3.5 km above the transition zone completely mixes the water. The most likely agency to initiate the ascending response (Figure 3, No. 2) by the larvae would be the change in the character of the tidal flows caused by shoaling of the bottom rather than agencies peculiar to the estuary. Herring are retained throughout their larval life over the banks and ledges of the open waters of the Gulf of Maine where the water is shallow and the tidal flows are well developed but conditions are not estuarine. After a brief transport downstream near the surface the larvae would resume their usual transport by descending towards the bottom.

The results suggested that the arrangement of buoyed and anchored nets in the estuarine channel was appropriate to sampling larval herring transported within the tidal currents. Larvae were sampled efficiently on both the flood and ebb tides, since no important main effect was obtained for tidal phase during the experiments. To obtain such an effect would have required a larval concentration to pass beyond the positions of the nets; then the larvae would either have to miss the nets on the return tidal current or drift to some area in the channel where they were not subject to the currents. Because the larvae were transported by the tidal currents, tide was always one of the interacting factors and an interaction between depth and location was not obtained.

One explanation for the appropriateness of the sampling design was that concentrations of the larvae were of sufficient length to overlap a pair of nets when transported into a given location. When this occurred, the difference in catch rates between the two lines of nets within the location would be small, and the difference between the two lines of nets in the other location where the concentration did not occur would also be small. These differences within the locations provided a measure of experimental error in the sampling design and if small they would yield a statistically significant F-ratio when compared to differences in catch rates between location and depth and the interaction of these two factors with tidal phase (e.g., F = mean square between locations/mean square within locations). Statistical significance would not occur when a concentration overlapped only one line of nets in a given location; the differences in catch rates between the two lines of nets would be relatively large, as indicated for the exterior and interior nets of the seaward location in Table 3.

Although net tidal flows in the channel affected the transport of the larvae, temporal variations in tidal currents made it difficult to determine the exact nature of that transport. The catch rates and corresponding tidal excursions obtained from the nets were accumulative and

TABLE 3.—Larval catches per 100 m^3 of water strained from an experiment during March 28, 1968. When treated as in Table 1 the distributions of the catch rates were not statistically significant.

Tide	Depth	Seaward location		Landward location	
Flood	Shallow	2.35	7.74	4.46	4.32
	Deep	2.68	2.84	3.85	3.65
Ebb	Shallow	1.37	6.07	3.38	3.58
	Deep	1.40	11.09	3.79	5.87

did not represent the many changes that probably occurred in tidal currents with time. These currents change not only their velocity but their type of flow as well (Graham and Venno, 1968).

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