Mortality, Growth, and Transport of Larval Atlantic Herring *Clupea harengus* in Maine Coastal Waters

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Abstract

Microstructural growth increments in otoliths of autumn-spawned, larval Atlantic herring from the Sheepscot River estuary of western Maine and Sullivan Harbor of eastern Maine provided estimates of mortality, growth, or transport times (or combinations of these) for 19 cohorts in 1980–1982. Mortality within seven cohorts averaged 2%/d (range, 0.7–3.1%/d). Growth (12 cohorts) averaged 0.199 mm/d (0.123–0.270). Transport times of larvae hatched on the spawning ground of eastern Maine and captured in the harbor and estuary (8 cohorts) averaged 16.5 d (5–35 d). Estimates of mortalities agreed ($P > 0.05$) with those from multicohorts obtained in the 1960s and 1970s (0.4–3.2%/d). Among the cohorts, extremes of larval growth differed significantly ($P < 0.05$), but most were similar and showed a weak trend toward slower growth in 1980–1982. No difference in growth ($P > 0.05$) was noted between larvae of cohorts spawned relatively early and those of a cohort spawned late. Larval mortality and growth appeared inversely correlated ($P < 0.05$) for seven cohorts. Variability in transport times was seven-fold, suggesting a wide dispersal of larval cohorts throughout the coastal water while in transit from the spawning grounds to inshore areas of retention. Possibly, different members of the same cohort from the eastern coastal spawning ground moved 95 km (straight-line distance) in 8 d to Sullivan Harbor and also 273 km to the Sheepscot estuary in 35 d. Although larval recruitment mechanisms are manifested inshore, it is suggested that such mechanisms are anticipated through cohort development in the coastal water.

Atlantic herring provided large harvests of juveniles in Maine during the 1950s: 34,400–90,600 t per year. Harvests declined in the 1960s to a low of 6,500 t in 1971, then fluctuated between 12,700 and 41,300 t. In 1983, even a low harvest of 12,400 t was possible only by fishing purse seines along the coast, because fixed gears (weirs and stop seines) were not effective. Apparently, juveniles were not only few, they were not available to the inshore fixed gear. Fixed gear usually contributes most of the harvest of juvenile fish aged 1–3 years, of which age 2 is the most desirable for canning as sardines.

Since 1975, the Maine Department of Marine Resources has forecast the harvest of 2-year-old Atlantic herring by the Maine fishery from the dynamics of autumn-spawned larvae along the coast (Graham 1982). These forecasts have been within 1–55% of subsequent harvest weights and 16–35% of harvest numbers; weight estimates were more variable because growth rates could not be anticipated. Harvests of the 1982–1983

juvenile fisheries were forecast within 1–4% by weight and 16–25% by number, and the fishing industry was warned of the collapse of the 2-year-old stock for the 1983 harvest. Forecasting depended, in part, upon detection of relatively late spawning (late October–November) which was believed to increase survival and to enhance recruitment (Graham 1982). Such late spawning was evident in 1974–1976 from the appearance inshore of small larvae during winter as well as autumn, when most newly hatched larvae were transported shoreward from coastal spawning grounds. Production of larvae declined after 1977 and the use of temporal progressions of modal lengths in frequency distributions to estimate growth and identify cohorts became complex. Since 1978 detection of early and late cohorts has depended upon the microstructural growth increments in otoliths for back-calculation of spawning dates (Townsend and Graham 1981). In addition, some information on the status of coastal spawning populations was inferred from
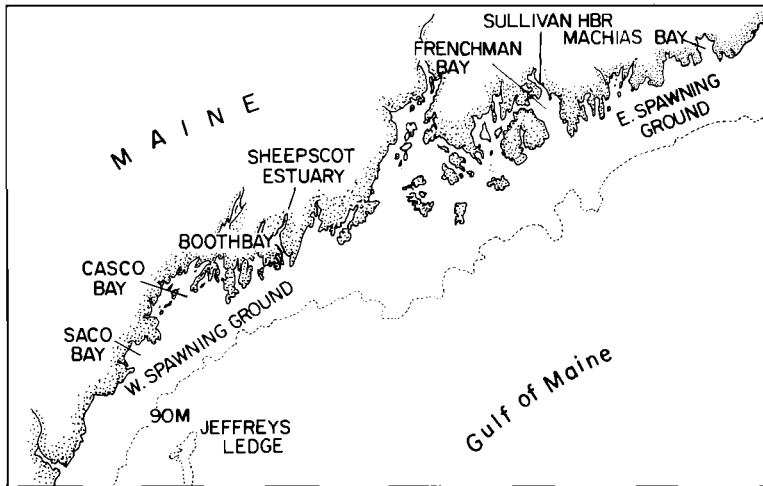
FIGURE 1.—*Study area for Atlantic herring along the Maine coast.*

research on larvae from cohorts (Graham et al. 1984). Qualitatively, larval cohort analysis has become progressively more important in such forecasts and inferences. To increase its application, this paper quantifies growth and mortality within larval cohorts during September through February and infers their transport times from a spawning ground to locations of inshore retention.

Study Area and Methods

Sampling and Processing Techniques

This paper concerns larval Atlantic herring hatched primarily during September and October from two spawning grounds along the Maine coast (Fig. 1). Larvae from the eastern ground, in addition to entering inshore waters adjacent to that area, are transported westward at least as far as the Sheepscot River estuary. Most appear to overwinter in estuaries and embayments, although a few remain in the coastal waters. Metamorphosis to their juvenile form occurs primarily in late spring. The two inshore areas sampled during the autumn and winter were the Sheepscot estuary in western Maine and Sullivan Harbor of eastern Maine (Fig. 1). Buoyed and anchored nets were used to strain the larvae from tidal flows during darkness (Graham 1982). Three lines each were buoyed and anchored one behind the other at the landward and seaward ends of a long (8 km) narrow channel in the lower estuary. Four plankton nets were fished from a given line, one

each at the surface, the bottom, and at depths of 10 and 15 m. The latter two nets sampled over the intervening uniform depth (60 m) of the channel with the rise and fall of the tide. Flow meters in the 24 nets recorded the amount of water strained to capture larvae from the ebb and flood tidal phases over a complete semidiel tidal cycle.

Operations in the harbor were similar to those in the estuary except in some placements and depths fished by the 20 nets. Two lines were fished one behind the other at the landward end of a long (2 km) narrow subtidal channel with nets at the surface and bottom, but the intervening depths were 3 and 10 m. At the seaward end of the channel, two lines were fished with nets at the same depths except that the bottom net was at 60 m compared to 40 m at the landward end. In addition, two lines positioned nets at the surface and bottom (3 m) within the constricted seaward entrances to the subtidal flats bordering the channel.

Thirteen overnight sets were made in the estuary: two each during October and November and three each during December, January, and February. Eight sets were made in the harbor; two each during September through December (Graham 1982). Net cod ends were collected at dawn, placed on ice, and brought to the laboratory where larval herring were sorted from them. Usually 10 larvae from each net sample were frozen immediately for otolith analysis. During 1982, only a few larvae were frozen in
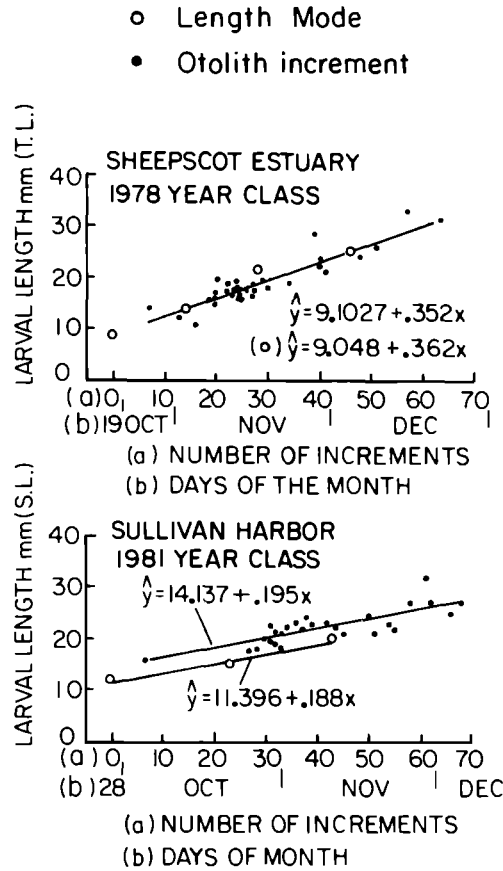
FIGURE 2.—*Two examples of agreement in growth of larval Atlantic herring as indicated by modal lengths and otolith increments. The position of "0 increment" is fixed arbitrarily to correspond with the first modal length. The 1978 least-squares regression line for modal length was omitted for clarity. Data for 1978 are from Townsend and Graham (1981). TL = total length; SL = standard length.*

TABLE 1.—*Cohorts of larval Atlantic herring captured in Sheepscot estuary and Sullivan Harbor and identified by back-calculating the date of fourth increment formation on otoliths. Estimates obtained are mortality (m), growth (g), and transport (t).*

Number	Capture location	Date of fourth increment	Estimates obtained
		1980 year class	
1	Sheepscot	1–15 Sep	
2	Sheepscot	15–30 Sep	mg
3	Sheepscot	1–18 Oct	mgt
4	Sheepscot	22 Oct–22 Nov	g
5	Sheepscot	23 Nov–6 Dec	
6	Sullivan	13–23 Sep	t
7	Sullivan	3–13 Oct	t
		1981 year class	
8	Sheepscot	3 Sep–10 Oct	mg
9	Sheepscot	15 Oct–3 Nov	mg
10	Sullivan	15 Sep–5 Oct	gt
11	Sullivan	6–23 Oct	gt
		1982 year class	
12	Sheepscot	15–28 Sep	mg
13	Sheepscot	29 Sep–12 Oct	mg
14	Sheepscot	13–27 Oct	g
15	Sheepscot	28 Oct–6 Nov	mg
16	Sheepscot	7–29 Nov	
17	Sullivan	19–28 Sep	t
18	Sullivan	29 Sep–26 Oct	gt
19	Sullivan	27 Oct–5 Nov	t

December from Sullivan Harbor and they were not processed. Otoliths were processed after the manner of Townsend and Graham (1981). Two counts of the microstructural growth increments were made on an otolith from a given larva. For the 1980 and 1981 year classes, these counts were averaged when the difference between them did not exceed 5% of the larger count; otherwise, they were rejected. Usually, the maximum difference did not exceed three increments. For the 1982 year class, an ocular micrometer was used to divide an otolith into visual "compartments," within which the number of increments was counted with a moving hairline. If the difference between two total counts exceeded 5% of the larger count, the error was corrected by compartment before the mean of the two total counts was accepted. Larvae were measured from the tip of the jaw to the end of the caudal peduncle (standard length) after they were thawed.

Cohort Identification

To identify cohorts of larvae, we had to assume that increments are added daily to otoliths of Atlantic herring. Lough et al. (1982) and Geffen (1982) have shown that this assumption may not apply for the addition of the first three increments and for some populations, respectively. However, we have some evidence to support it for Maine larvae. Growth rates usually are difficult to estimate from progressions of length-frequency modes, because they become distorted by mortality and new immigration into the sampling area, but two successful estimates are shown in Fig. 2. Corresponding growth rates estimated from otolith increments have slopes nearly identical to those for modal lengths. When the regressions are superimposed, an otolith accretion rate of about one increment per day is apparent from
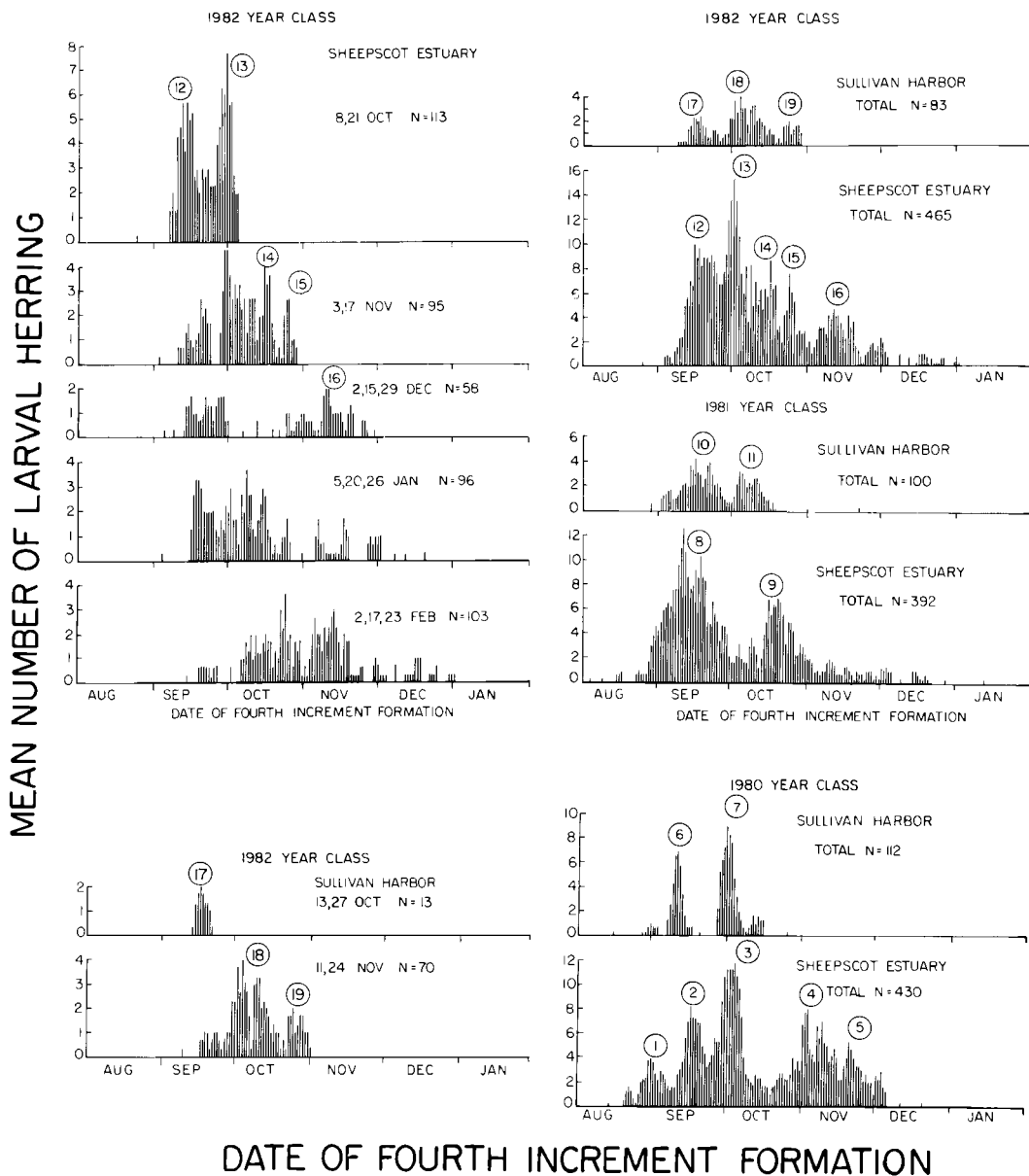
DATE OF FOURTH INCREMENT FORMATION

FIGURE 3.—*Atlantic herring abundance frequencies used to identify cohorts (circled numbers; see Table 1) based on back-calculated dates of fourth otolith increment formation. "Values" are 3-d moving means, three increments being about the maximum error in increment counts. Data for 1980 and 1981 are from Graham et al. (1984).*

comparison of time and increment scales along the abscissa. When growth of larvae slows, as it does in late January and early February, this is reflected both by increment counts (Townsend and Graham 1981) and by mean and modal lengths (Graham et al. 1972).

Lough et al. (1982) found that northwestern

Atlantic herring larvae possibly required as many as 22 d to form the first three otolith increments in the laboratory, after which accrual was daily as indicated by field data. Geffen (1982) did not observe this delay in formation of the early increments within a reared population of northeastern Atlantic herring and could not obtain a

daily rate of accrual. Because of the uncertainty surrounding formation of the first few increments, it was assumed that their period of formation was relatively constant for the purposes of this paper. Evidence obtained from the spawning ground in eastern Maine (Fig. 1) during the autumn of 1982 suggested that the fourth increment formed as larvae reached about 12 mm, when the alongshore drift of the larvae began. Recently hatched larvae (8–10 mm) were concentrated near a spawning site, although somewhat dispersed. These larvae rarely showed an increment. The examination of larger larvae, which had drifted westward from the spawning site, showed that larval length was linearly related to the number of otolith increments ($r = 0.97$) from about 12 mm and about 2 increments on.

We identified 19 cohorts for year classes 1980–1982 from the back-calculated dates at which the fourth increment was formed (Table 1; Fig. 3). Delineation of cohorts from abundance frequencies is subjective; assigned duration of cohort formation ranged from a few days, when cohorts were strong and discrete, to several weeks, when the opposite was true. Only total plots of abundance frequencies are shown in Fig. 3 for the 1980–1981 year classes; monthly plots are given by Graham et al. (1984).

Mortality, Growth, and Transport

Calculation of catch rates for a cohort required extrapolation from the measured subsamples. Subsample data first were pooled over the two or three sampling dates each calendar month. The proportion of the pooled subsample represented by each cohort was determined. Finally, the average overall catch rates for the month (total larvae per 100 m³ of water strained by the nets) was multiplied by cohort proportions to obtain monthly cohort catch rates (Gulland 1966). These values were assigned to the midpoint date within the monthly sampling sequence and mortality was calculated as the percent decrease in catch rate over time. We assumed that larvae of a given cohort neither immigrated to nor emigrated from the sampling area during the period of calculation. During past surveys, the movement of larvae shoreward was traced by Graham et al. (1972), but no seaward movement subsequently occurred. Shoreward transport of larvae ceased a short distance (2 km) landward of the sampling sites in the estuary and harbor because

of shoals and tidal falls that eliminated systematic tidal flows. In the estuary, some larvae moved landward of the sampling area into a small harbor, which was connected to a channel paralleling that of the estuary; however, progression of catch rates with time in the two channels was similar, suggesting that channels were populated largely and independently from their seaward ends (Graham 1982). Graham and Davis (1971) found that immigration of the larvae occurred when the larvae were aggregated and that as these aggregations were depleted and dispersed immigration appeared to cease. Only those cohorts which reached a peak in numbers of larvae followed by an uninterrupted decline during 3 months or more were used in our calculations of mortality.

Growth rates within cohorts came from linear regressions of larval length against number of otolith increments. The regressions fit arithmetic data ($r > 0.90$) better than logarithmically transformed data in all but one case. The regressions were first compared by analysis of variance and then their slopes were compared by the Student–Newman–Keuls range test (Zar 1974). Data entering the regressions were restricted to larvae with at least 11 otolith increments, and to cohorts represented in at least two successive months (with one exception: cohort 18; Fig. 3) and by at least 40 increments. Analyses were not extended into January when growth is known to slow.

Transport time was estimated from the total counts of increments beginning at increment 4, when alongshore drift of the larvae began. To place transport within a time frame, the arrival date of larvae at the harbor or estuary was considered as the mid-date between times when larvae of a given cohort were not present in the samples and their first capture. We estimated transport time for those larvae whose origin was reasonably certain, primarily those captured in Sullivan Harbor. However, a comparison of abundance frequencies for the 1980 year class (Fig. 3) suggested that cohorts 3 and 7 were both from the eastern spawning ground, thus times were estimated for both sampling areas (Graham et al. 1984). Survey data collected in 1972 (Graham 1982), in 1980 (Graham et al. 1984), and in 1982 (Townsend et al., in press) suggested (1) that larvae drifted westward from the eastern spawning ground and (2) that this was the only major ground east of Sullivan Harbor and perhaps east of the western spawning ground off Boothbay and Saco Bay (Fig. 1).

TABLE 2.—*Mortality estimates for cohorts of larval Atlantic herring in the Sheepscot estuary during autumn and winter, 1980–1982.*

Sampling mid-date	Number of larvae analyzed		Proportion in cohort	Mean catch rate, number/100 m³		Cohort mortality, %	
	Total	Cohort		Total	Cohort	Interim	Daily
Cohort 2 (15–30 Sep 1980)							
14 Nov	140	37	0.264	5.08	1.44		
12 Dec	118	3	0.025	7.25	0.18	86.3	3.1
18 Jan	64	1	0.016	2.18	0.03	81.6	2.2
Cohort 3 (1–18 Oct 1980)							
14 Nov	140	94	0.671	5.08	3.41		
12 Dec	118	17	0.144	7.25	1.04	69.3	2.5
18 Jan	64	4	0.062	2.18	0.14	87.0	2.4
Cohort 8 (3 Sep–10 Oct 1981)							
12 Oct	97	97	1.000	2.74	2.74		
10 Nov	66	30	0.454	1.14	0.52	81.2	2.8
12 Dec	52	21	0.404	0.75	0.30	41.7	1.3
17 Jan	57	46	0.807	0.28	0.23	24.4	0.7
16 Feb	46	37	0.804	0.22	0.18	22.9	0.8
Cohort 9 (15 Oct–3 Nov 1981)							
10 Nov	66	36	0.546	1.14	0.62		
12 Dec	52	31	0.596	0.75	0.44	28.1	0.9
17 Jan	57	11	0.193	0.28	0.06	87.6	2.4
16 Feb	46	9	0.196	0.22	0.04	23.7	0.8
Cohort 12 (15–28 Sep 1982)							
14 Oct	108	50	0.463	3.74	1.73		
10 Nov	94	16	0.170	3.02	0.51	70.5	2.6
16 Dec	53	12	0.226	0.43	0.10	80.8	2.2
Cohort 13 (29 Sep–12 Oct 1982)							
14 Oct	108	58	0.537	3.74	2.01		
10 Nov	94	33	0.351	3.02	1.06	47.3	1.7
16 Dec	53	11	0.208	0.43	0.09	90.6	2.5
Cohort 15 (28 Oct–6 Nov 1982)							
10 Nov	94	10	0.106	3.02	0.32		
16 Dec	53	7	0.132	0.43	0.06	81.9	2.3
16 Jan	86	6	0.070	0.52	0.04	88.1	2.8

Results

Estimates of mortality did not vary greatly among larval cohorts from the Sheepscot estuary (Table 2). Daily mortality averaged 2% and ranged from 0.7% to 3.1%; it did not differ among years or among cohorts within a year (Kruskal–Wallis test; $P > 0.05$).

Pooled over 3 years (1980–1982), 3–4 months (September, October–December), and 12 cohorts, larval growth rates averaged 0.199 mm per increment, with a standard error of ±0.004 mm. Significant differences (Table 3) occurred among cohorts despite heterogeneity of variances (Bartlett's tests, $P < 0.05$, the results of which were unaffected by logarithmic transformation of the data). Superimposed on a broad similarity of growth among larval year classes, there was a weak trend toward slower growth from 1980 to 1982. A typical plot of length against increment count for a year class and its division by cohort is shown in Fig. 4.

Inferred transport times of larval herring from the eastern spawning ground varied widely (Table 4). In one instance, larvae from the same year class (1982) and arrival date (November 4) had transport times of 5 and 22 d. Assuming that cohorts 3 and 7 were aggregations from the same cohort, as indicated by their similar dates of fourth increment formation (Fig. 3), their transport to the estuary required an additional 27 d beyond that necessary for them to reach the harbor from the eastern spawning ground.

Discussion

Previous mortality estimates for larval Atlantic herring from the Sheepscot estuary involved

TABLE 3.—*Estimates of growth rates (slope) for cohorts of Atlantic herring larvae from Sheepscot estuary (E) and Sullivan Harbor (H) as indicated by linear regression of length (dependent variable) on otolith increments. Slopes without a letter in common are significantly different (Student–Newman–Keuls test; P ≤ 0.05).*

	Cohort number	Period covered	Number of larvae	Regression		
Year class				Intercept	Slope ± SE	
1980 E	2	Oct–Dec	59	9.232	0.271 ± 0.036	a
1980 E	3	Oct–Dec	73	11.490	0.220 ± 0.035	b
1980 E	4	Nov–Dec	87	11.469	0.240 ± 0.038	ab
1981 E	8	Oct–Dec	117	12.726	0.199 ± 0.033	b
1981 E	9	Nov–Dec	63	13.836	0.123 ± 0.037	c
1981 H	10	Sep–Dec	45	12.947	0.205 ± 0.035	b
1981 H	11	Oct–Dec	26	14.137	0.195 ± 0.040	bc
1982 E	12	Oct–Dec	61	18.820	0.194 ± 0.034	c
1982 E	13	Oct–Dec	72	14.732	0.210 ± 0.034	b
1982 E	14	Nov–Dec	31	13.637	0.220 ± 0.040	b
1982 E	15	Nov–Dec	15	14.395	0.177 ± 0.041	bc
1982 H	18	Nov	41	14.621	0.196 ± 0.033	bc

larvae from several, rather than individual, cohorts. Estimates made in the mid-1960s to early 1970s were low (0.4–3.2%/d), but the variation they implied appeared sufficient to affect considerably the size of the larval population in the spring just prior to their metamorphosis and, to a degree, the recruitment of age-2 juveniles to the sardine harvest (Graham 1982). Measurement of mortality was based on statistical support for the assumption that shoreward migration of larvae from all cohorts ceased by early December (Graham and Davis 1971). In the mid-1970s and in most succeeding years, the greater frequency of late spawning and, thus, late shoreward migration (e.g., cohorts 4–5; Fig. 3) made this assumption untenable for some cohorts and the collective estimates were abandoned. Winter mortalities for individual cohorts from 1980–1982 year classes were similar (0.7–3.1%/d) to earlier, collective estimates, as indicated by the Mann Whitney U-test ($P > 0.05$). Perhaps, as in the past, the collective variability in the winter mortalities of individual cohorts affected recruitment, but an additional important factor may be late spawning that shortens the period of winter mortality, as hypothesized by Graham (1982).

During 1964–1973, the catch rate of larval Atlantic herring at the beginning of winter was correlated with subsequent recruitment of 2-year-olds to the sardine harvest (Graham 1982). The relatively low catch rate in early winter followed an apparent abrupt 10-fold mortality for those larvae that had migrated shoreward and accumulated in the upper ends of lower estuaries and embayments during autumn (Graham et al. 1972). Beginning in 1978, peak catch rates of such autumnal accumulations were reduced at least by half (Graham et al. 1984). During 1980–1982, peak catch rates of individual cohorts during autumn were very low, 0.32–3.41 larvae/100 m³ (Table 2) and autumnal mortality estimates were equivalent to those of previous winters, as indicated by the Mann–Whitney U-test ($P > 0.05$). In one case, the 1981 year class, a comparison of catch rates for all larvae in early December with previous classes appeared feasible. Relatively late spawning and late shoreward immigration were almost absent in 1981 (Graham et al. 1984). Catch rates of previous classes varied from 0.47 to 5.75 larvae/100 m³; that of the 1981 year class was 0.45. Apparently, the low mortality of the cohorts did not compensate fully for the poor production of larvae in the autumn, as indicated by subsequent failure of this year class in the sardine fishery.

Not all larvae experience a winter slowdown in growth during late January and early February (Townsend and Graham 1981). The abundance of some larvae apparently declines so rapidly in the autumn that few of their cohort are present by winter. However, length-frequency progressions from previous research (Graham 1982) indicate that the survivors of such cohorts are of large size by winter. They vary in standard length from 40 to 50 mm as early as December. Occasionally, they occur as recently metamorphosed juveniles in our nets during winter. Cohort 1 (Fig. 3) may be an example of such an occurrence. Relatively early and late-spawned larvae sometimes grow at significantly different rates. Jones (1983) reported differences between early and late-spawned larvae of cohorts during
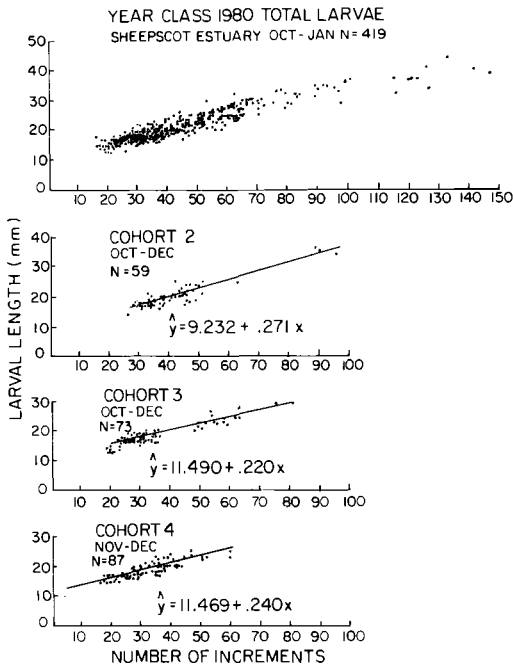
FIGURE 4.—*An example of the growth of larval Atlantic herring within a year class and its cohorts.*

TABLE 4.—*Estimated transport time for cohorts of larval Atlantic herring arriving in Sheepscot estuary (E) and Sullivan Harbor (H).*

Cohort number	Year class	Arrival date	Transport days
6	1980 H	1 Oct	13
7	1980 H	16 Oct	8
3	1980 E	13 Nov	35
10	1981 H	22 Sep	7
11	1981 H	14 Nov	30
17	1982 H	5 Oct	12
18	1982 H	4 Nov	22
19	1982 H	4 Nov	5

Gamble et al. (1981) and Rosenberg and Haugen (1982), respectively. We discarded the possibility that the plot in Fig. 5 resulted from autocorrelation, although the same data sets of otolith counts were involved in calculations of growth and mortality. If sufficient data were available, the growth rates could be obtained from length-frequency modes as well as from increment counts (Fig. 2).

Transport of larvae away from their hatching sites may increase their chances for survival. Lambert (1984) suggested that a succession of cohorts of larval Atlantic herring hatched over time and space served to limit intraspecific competition and divided a limited food supply more equitably among the total population. Townsend et al. (in press) demonstrated that westward transport of the larvae from the eastern Maine spawning ground (Fig. 1) during 1982 brought the larvae into an area of abundant food supply. The large variation among estimates of transport times (Table 4) for larval cohorts indicated their
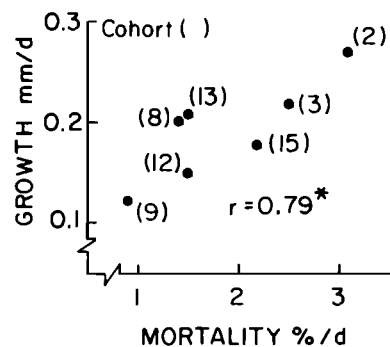
1978 in the Sheepscot estuary, using data from Townsend and Graham (1981). She suggested that a statistically significant difference in growth existed between them, the late-spawned larvae growing more slowly. In Table 2 of this paper, such a comparison is possible only in one instance, during 1980. Cohort 4 (late spawned) overlaps in statistical range the fastest growing cohort (2) and many of those growing more slowly (early spawned).

The relation between growth and mortality of larvae in the estuary may be complex. Data from year classes 1976–1978 (Graham 1982) suggested that immigrating larvae lost weight as they accumulated to a peak in estuarine abundance. But subsequent mortality and decline from this peak coincided with a gain in weight by the relatively few survivors. Perhaps an analogous relation was indicated by the mortality and growth of larvae from the 1980–1982 year classes. Subsequent to a peak in catch rate, larvae in cohorts with higher mortalities grew at a faster rate and those with lower mortalities grew at a slower rate (Fig. 5). Such agreement could be caused by differential culling of weaker, slower-growing larvae from the cohorts through either predation or starvation, as indicated by the experiments of

FIGURE 5.—*Comparison of mortalities (Table 2) and growth rates (Table 3) for cohorts of Atlantic herring during October–December. The correlation coefficient (r) is significant at P≤0.05 (asterisk).*

extensive dispersal along the coast and potential reduction of intraspecific competition. For example, representatives of perhaps the same cohort of the 1980 year class (numbers 3 and 7; Table 4) were transported (straight-line distance) about 95 km to the harbor in one case, and 273 km to the estuary in another.

Hatching over the spawning ground, transport from the ground, autumnal accumulation in inshore retention areas, and winter mortality constitute a series of preludes to larval metamorphosis in the spring. During the present period of low spawning stock (Graham et al. 1984), it is unlikely that a given determinant of recruitment operates only within a single prelude. For example (Fig. 5), despite faster growth, inshore mortalities of cohorts 2 and 3 (1980) were higher than those for cohorts 8 and 9 (1981). Taken alone, one might anticipate a larger recruitment of age-2 juveniles to the sardine fishery in 1983 than in 1982. However, the low production of larvae and the absence of late-spawned cohorts in 1981 (Fig. 3) led, in 1983, to one of the poorest sardine harvests (age 2) in 100 years (Graham et al. 1984). The dispersal of larvae along the coast and the relative lateness of spawning there are considered important to recruitment of sardine herring (Graham 1982). These recruitment mechanisms are manifested inshore, but their development occurs in coastal waters, where they are presently under study (Townsend et al., in press).

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