

ABUNDANCE, DISTRIBUTION, MOVEMENTS, AND LENGTHS OF LARVAL HERRING ALONG THE WESTERN COAST OF THE GULF OF MAINE

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ABSTRACT

This paper describes the abundance, distribution, movements, and lengths of larval herring along the western coast of the Gulf of Maine. Larvae were most numerous in the catches throughout the coast in the autumn, reached a low in the winter, and increased in the spring. Growth in the autumn is estimated at 1 to 1.3 mm per 5-day intervals. Larval mortality was highest in the autumn, lower in the winter, and lowest in the spring. The mortality in the winter usually varied with their condition and determined the subsequent level of spring abundance. We selected three different types of estimates as desirable for predicting the recruitment of immature herring to the sardine fishery of Maine: (1) winter mortality, (2) larval condition in the winter, and (3) spring abundance.

The commercial catch of 2-year-old Atlantic herring, *Clupea harengus harengus* Linnaeus, fluctuates annually along the western coast of the Gulf of Maine. The Maine sardine industry processes these immature herring, but cannot anticipate the amount of fish available for canning each year. One approach to this problem is to determine whether the abundance of herring during their first year of life is related to the number of fish entering the fishery. To establish whether such a relationship exists, the desirable estimate of abundance or its correlative must be determined first. We describe the distribution, abundance, movements, and lengths of larval herring along the western coast of the Gulf of Maine. We discuss the seasonal changes in larval abundance caused by their mortality and the relation of the sources of larvae to their distribution and movements. From these analyses we selected three types of estimates: (1) winter mortality, (2) larval condition in the winter, and (3) spring abundance.

Larval herring occur throughout the Gulf of Maine-Georges Bank area. They concentrate in the offshore bank area (Tibbo et al., 1958); along the southeastern coast of Nova Scotia

(Das, 1968)²; and the western coast of the Gulf of Maine (Graham and Boyar, 1965). During their relatively long larval period, herring may drift with the residual currents about the banks and in the Gulf (Colton and Temple, 1961; Das, 1968, see footnote 2). Racial studies show that these larval herring have three parental stocks; namely, Georges Bank, the southern coast of Nova Scotia, and the western coast of the Gulf of Maine (Anthony and Boyar, 1968; Ridgway, Lewis, and Sherburne, 1969). The relation between the parental stocks and the larvae is not clear.

In the Boothbay area of the Maine coast, herring were found in estuaries and embayments throughout their larval life (Graham and Boyar, 1965). In this area larval catches reached a peak in the autumn shortly after hatching and declined to a minimum during winter. Catches were sporadic in the spring and in May the fish metamorphosed. Evidence that in the spring the larger larvae avoided our conventional sampling gear (Gulf III and meter nets) led to the development of the Boothbay Depressor trawl (Graham and Vaughan, 1966) and buoyed and

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² Das, N. 1968. Spawning, distribution, survival, and growth of larval herring (*Clupea harengus* L.) in relation to hydrographic conditions in the Bay of Fundy. Fish. Res. Board Can., Tech. Rep. 88, 129 p.

anchored tidal nets (Graham and Venno, 1968). Catches with this gear provided information on mortality in an estuary (Graham and Davis, 1971), condition (Chenoweth, 1970), and seasonal feeding (Sherman and Honey, 1971). Coastal salinity, temperature, and currents were measured during zooplankton surveys (Sherman, 1970) and hydrographic surveys (Graham, 1970a, b).

MATERIALS AND METHODS

Larval herring were sampled in two areas (Figure 1): A coastal area which extended from the headlands to 20 km offshore (50-fm isobath) along the coast from Cape Ann, Mass., to Machias Bay, Maine; and the Boothbay area which extended to 6.5 km offshore (lat $43^{\circ}45'N$) and was bounded by the Sheepscot and Damariscotta estuaries. Collections were made once or twice each season in the coastal area from autumn 1962 through spring 1967; and every other week

in the Boothbay area from autumn 1964 through spring 1967. Additional collections, obtained after 1967, will be cited when pertinent. There were 21 stations in the coastal area until the spring of 1965 when the number was increased to 46 to provide more adequate data. In autumn 1966, the area was divided into 30-min squares of latitude and longitude and the squares subdivided into quarters. The 46 quarters sampled on a given cruise were selected randomly. An exploratory winter cruise (1964) was made within the coastal bays and estuaries and two cruises were made in the Boothbay area in early March of 1964 and 1965. In the Boothbay area, samples were obtained in all locations that were navigable for the 13-m vessel, *MV Phalarope*.

Larval herring were collected by the methods listed in Table 1. We captured small larvae in the autumn with a Gulf III sampler (Gehringer and Aron, 1968) and larger larvae in the winter and spring with Boothbay Depressor trawls (Graham and Vaughan, 1966). Catches ob-

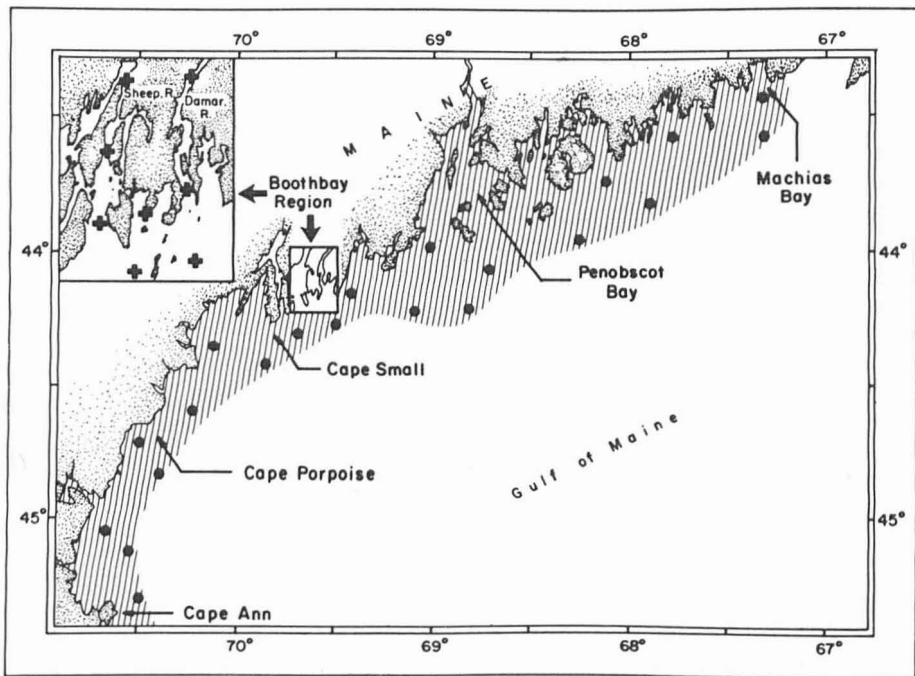


FIGURE 1.—The coastal (hatched) and Boothbay (enclosed) sampling areas along the western coast of the Gulf of Maine. Dots and crosses are station positions; S and D indicate the Sheepscot and Damariscotta estuaries.

TABLE 1.—Methods of sampling larval herring in the western Gulf of Maine, 1962-67. Volume sampled in 7½-min tow = given volume ÷ 4.

Area	Stations	Season	Gear type	Tow		Water strained	Towing velocity
				Depth	Duration		
Coastal	21-48	Autumn	Gulf III	0-10-20 ^m	30 ^{min}	200 ^{m³}	6 ^{knots}
		Winter-spring	Boothbay Depressor trawl				
			No. 1	0-10-20	30 (or 7½)	4,200 (1,050)	6
			No. 2	0-10-20	30	17,000	4½
			No. 4	0-10-20	30 (or 7½)	8,000 (2,000)	5
Inshore	8	Autumn	Gulf III	0-mid-depth- bottom	30	135	4½
		Winter-spring	Boothbay Depressor trawl				
			No. 1	0-mid-depth- bottom	30	12,800-4,200	4

¹ Dependent on mouth opening of liner.

tained were adjusted to the number of larvae captured per 100 m³ of water strained during a tow. During the coastal cruises the gear was towed obliquely for 30 min at each station (10 min each at the surface, at 10 m, and at 20 m) except on the coastal cruises after autumn 1966, when each of the 46 quarters was sampled with two oblique 7½-min tows (2½ min at the surface, at 10 m, and at 20 m). The direction of these two tows was selected randomly and catches were averaged to obtain an estimate of abundance. Filtration efficiencies of the sampling gear approached 100%. Comparisons between catch rates of the Gulf III and the Boothbay Depressor trawl differed on individual stations during tests covering the period of their exchange within the sampling program. However, the catch rates were similar for the two gear when they were averaged for stations or for an entire cruise. Experiments also showed differences in catch rates between short and long tows, between tows of different depths, and between tows made during nighttime and daytime. Only the differences between rates during nighttime and daytime were sufficiently important to the analyses of this report and they are given. Information on the length and depth of tow and comparisons of catch rates between the two gear are being prepared for publication.

Larval herring, preserved in 10% Formalin, were measured from the tip of the jaw to the

end of the caudal peduncle (standard length). Conversion of this measurement (SL) extended to total length (tip of jaw to the tip of the longest lobe of the caudal fin) (TL) may be made for larvae from 20 to 45 mm SL by:

$$TL = - 3.47 + 1.24 SL$$

RESULTS

HATCHING

Catches of recently hatched herring (4-9 mm) provide evidence that there are several spawning areas along the western coast of the Gulf of Maine, but that the time of hatching differs between the eastern and western sectors of the coast. Recently hatched larvae were captured throughout the coastal sampling area from late September until early November. Some of these larvae had yolk sacs, especially those obtained near the headlands of the Boothbay area, where the occurrence of hatching was monitored each year. Relatively large numbers of larvae were captured east of Cape Small in the early autumn and to the west of this Cape in late autumn (Table 2). The autumnal hatch along the coast was expected, since Boyar (1968) found that the gonads of most adult coastal herring reached spawning condition by late September in this area. Also Goode (1884) and Bigelow and Welsh

TABLE 2.—Coastal distribution of the number of recently hatched larval herring from late September to mid-October and from then to early November; water temperatures are from mid-October.

Area (Figure 1)	Percentage of larvae, 4-9 mm		Mean temperature (°C)	
	Sept.-Oct. 1962-63 (N = 267)	Oct.-Nov. 1962-66 (N = 1,872)	mid-October 1963	
			Surface	Bottom
Cape Ann- Cape Small	9	97	12	8
Cape Small- Penobscot Bay	54	2	11	9
Penobscot Bay- Machias Bay	37	1	9	10

(1925) reported that herring spawned in the western area later than in the eastern sector of the coast. Hatching of larvae in the spring was observed only once; three larvae (8-9 mm) were captured in the Boothbay area in May.

The earlier hatching in the eastern sector of the coast may be attributed to the distribution of water temperature. The average surface temperature from 1963 through 1965 was 9.1°C in the western sector of the coast and 6.2°C in the eastern sector. Bottom temperatures during the same period averaged 4.5°C in the western sector and 5.6°C in the eastern. Each year the surface water was 2° to 3.5°C warmer in the western than in the eastern sector, while the eastern bottom water was 1° to 1.5°C warmer than in the western sector. These temperature trends were established primarily in the summer (Graham, 1970a) and persisted into the autumn (Table 2). Possibly, cooler autumn surface temperatures in the eastern sector would initiate spawning sooner than in the western sector; warmer bottom temperatures would incubate the eggs faster (Das, 1968, see footnote 2).

SEASONAL ABUNDANCE, DISTRIBUTION AND MOVEMENTS

Larvae were most numerous in the catches throughout the coast in the autumn, reached a low in the winter, and increased slightly in the spring (Figure 2). Catches were largest in the eastern sector of the coast in early autumn, but larger in the western sector by mid-autumn. By late autumn, catches dropped drastically in both sectors and reached a common level throughout the coast. In the Boothbay area the numbers of

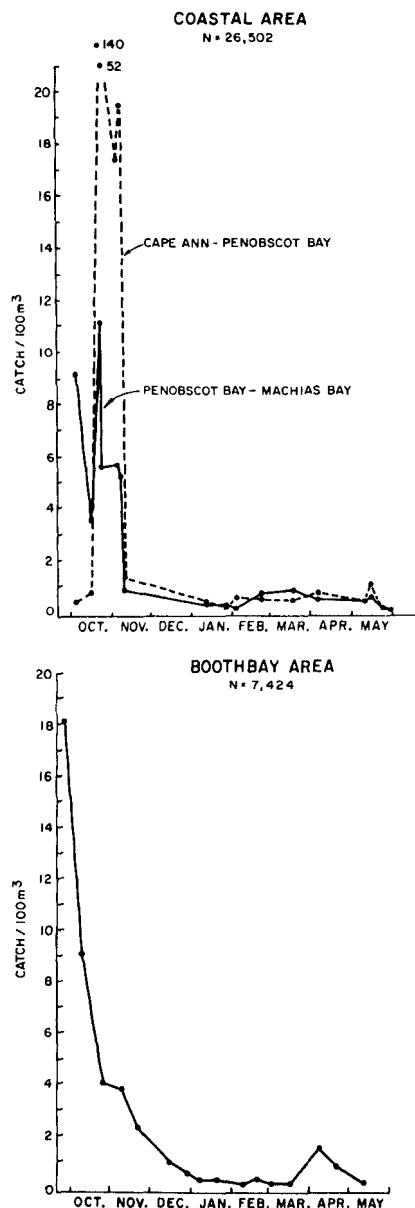


FIGURE 2.—Upper panel - mean catch rates of larval herring in the western (Cape Ann-Penobscot Bay) and eastern (Penobscot Bay-Machias Bay) sectors of the coast during cruises from 1962-67. Lower panel - mean catch rates from the Boothbay area for semimonthly periods combined for the years 1964-67. Points are plotted at the midpoint of the cruise periods.

captured larvae were also highest in the autumn, lowest in the winter with an increase in the spring. The timing of autumnal abundance varied between years and will be discussed in detail in the section on movements. As recorded by Graham and Boyar (1965) the Sheepscot estuary usually contained more larvae than the Damariscotta estuary. About 60-68% of the total catch was taken in the Sheepscot in a given year.

Seasonal changes in the dispersal of larvae were analogous to those of abundance. Larvae were aggregated in the autumn and spring and dispersed in the winter. For instance, catches during an autumn cruise had a coefficient of variation of 214%, during a winter cruise 17%, and during a spring cruise, 50%. Exploratory cruises showed that larvae were dispersed from the headlands to 28 km up the estuaries in the Boothbay area during early March when winter conditions still prevailed.

Changes in distribution occurred in the autumn and spring when the larvae moved landward. These changes were apparent when the average catch rates from the Boothbay area (\bar{x} Boothbay) were compared synoptically with those from cruises in the adjacent coastal area from Cape Small to Penobscot Bay (\bar{x} coastal). The synoptic catch rate from the Boothbay area was obtained by interpolating between rates of the biweekly cruises that occurred a few days before and after a given coastal cruise. The percentage catch rate of larvae in the Boothbay area [\bar{x} Boothbay/ \bar{x} Boothbay + \bar{x} coastal] \times 100 did not exceed 40% during October when hatching was at its peak, then reached almost 90% in November coincident with a decline in hatching (Figure 3). The percentage was again low in February and March, but increased to about 85% in April and May prior to metamorphosis. Similar comparisons between Boothbay data and those from coastal areas east and west of Boothbay did not yield these relations. Apparently, the shoreward shift in distribution was not synchronized along the entire coast.

Other movements of larvae were evident from an analysis of the data from the coastal and Boothbay areas. In autumn, an alongshore movement from east to west was apparent when

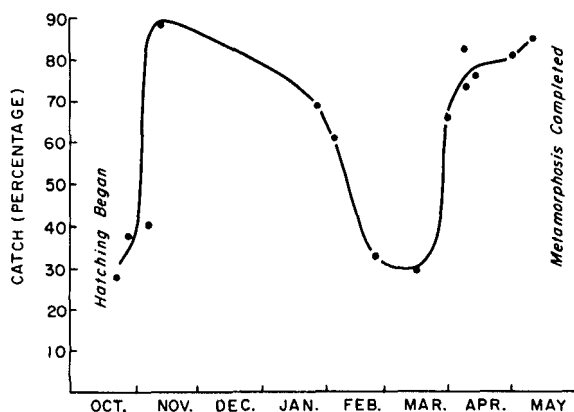


FIGURE 3.—The change in percentage in the average catch rate in the Boothbay area as compared with the average catch rate in the coastal area.

larvae were obtained in the Boothbay area that were larger than those recently hatched in the western coastal sector. The movement of larvae in the spring was marked by their accumulations in locations receiving shoreward intrusions of coastal water and by the relation of their distribution with that of surface salinity. The intrusions resulted from eddies formed by the spacing of river discharge along the western sector of the coast (feathered arrows, Figure 4). The configurations of isohalines and lines of equal larval density throughout the coast were often similar. Such similarity indicated that the magnitude of station-to-station differences in catch paralleled the station-to-station differences in salinity. These differences were accumulated for coastal stations from west to east and their frequency distributions were plotted on probability paper for two cruises having widely different salinity distributions (Figure 5). The cumulative frequencies of salinity and catch were alike for a given cruise, but differed between cruises. We infer from these results that the larvae are carried by currents, indicated by the station-to-station differences in salinity. The precise direction of drift cannot be ascertained because it is not possible to determine whether the salinity distribution is causing the current or is the effect of the current, perhaps generated by winds.

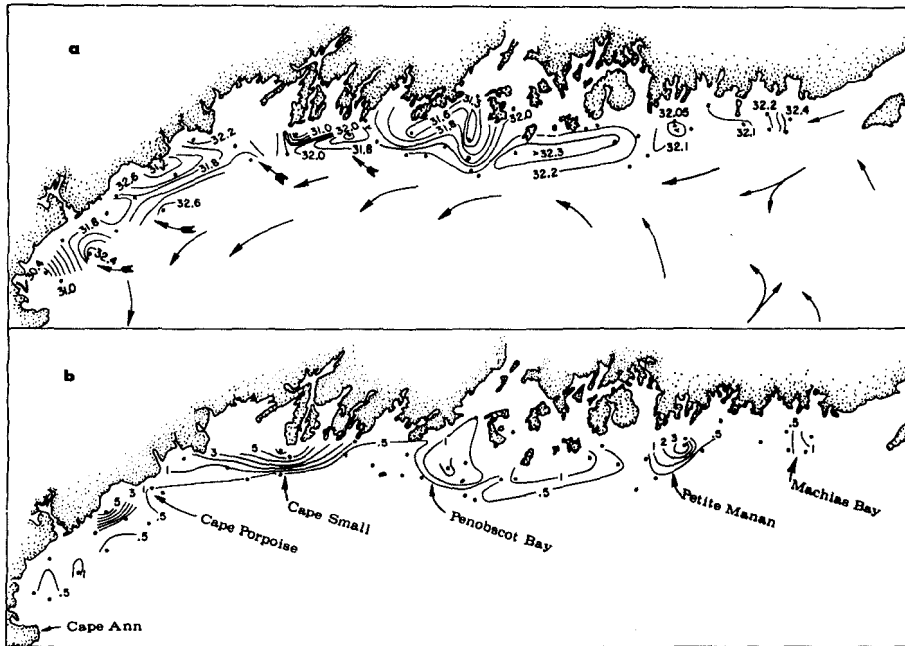


FIGURE 4.—(a) Isohalines (‰) during a spring cruise, March 28-April 13, 1967. Feathered arrows indicate shoreward intrusions of coastal water (from Graham, 1970b), and unfeathered arrows indicate current directions along the coast (from Bumpus and Lauzier, 1965). (b) Isolines of larval catch rates (no/100 m³) for the above cruise.

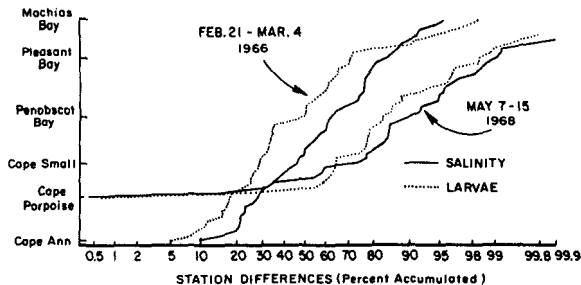


FIGURE 5.—Accumulated frequency distributions of station-to-station differences from west to east along the coast. The cruise in 1968 began to the east of that in 1966.

Larval movements up the estuaries during autumn were easier to detect in the Boothbay area because larvae were transported inshore primarily by tidal flows (Graham and Davis, 1971). Tidal flows followed the inshore-offshore axes of the estuaries and embayments; thus the landward movement was detected by grouping

catches made at the three outer estuarine, three lower estuarine, and two upper estuarine stations, and plotting them in a time series. Peaks in larval abundance progressed from outer to upper estuarine stations with time, suggesting an inshore movement of the larvae (A, B, and C in Figure 6). Two such progressions were obtained in 1966 and one in both 1964 and 1965. In 1964, larvae passed the outer and lower stations between our scheduled cruises and appeared first at the upper stations as a peak in abundance in early October. In spring, larvae were always more abundant at the upper estuarine stations, and progressions in peaks of abundance up the estuary were not apparent.

LARVAL LENGTHS

The rate of increase in average length varied seasonally and geographically. Data from the coastal and Boothbay areas showed a marked

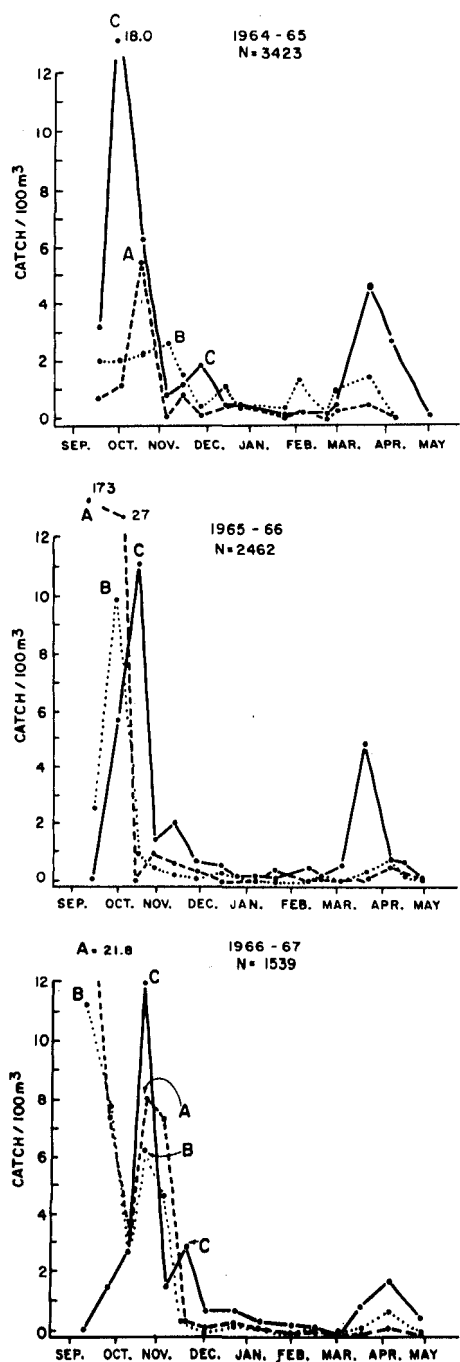


FIGURE 6.—Seasonal changes in larval abundance in the Boothbay area during 1964-67. Values are plotted for outer (A), lower (B), and upper estuarine (C) stations.

increase in length in the autumn followed by a more gradual increase in the winter and spring (Figure 7). During the autumn and spring the increase in length accompanied a comparable increase in weight, but not in the winter when the larvae were very thin (Chenoweth, 1970). In the coastal area the increase in length

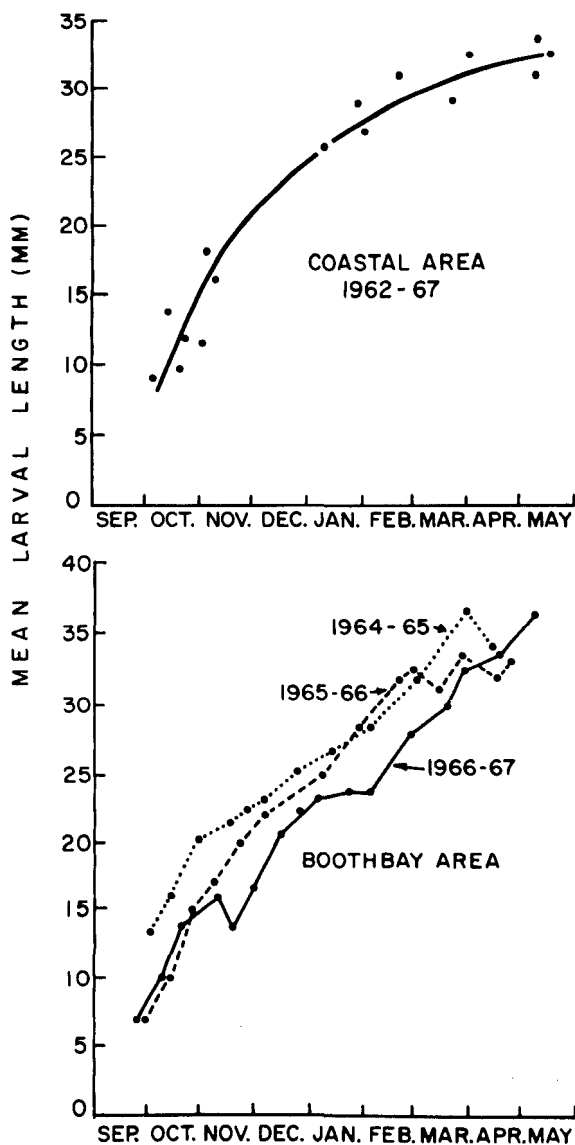


FIGURE 7.—Seasonal change of mean larval length in the Boothbay and coastal areas, 1962-67.

appeared asymptotic while the average length fluctuated above and below 32 mm in the Boothbay area from March through May in 1965 and 1966. Differences in the average length also occurred between the eastern and western sectors of the coast. In late September to mid-October, the mean lengths did not differ greatly along the coast (Figure 8). By early November the mean length was larger in the eastern sector than in the western sector, but this difference diminished in winter; by spring mean lengths were similar along the coast.

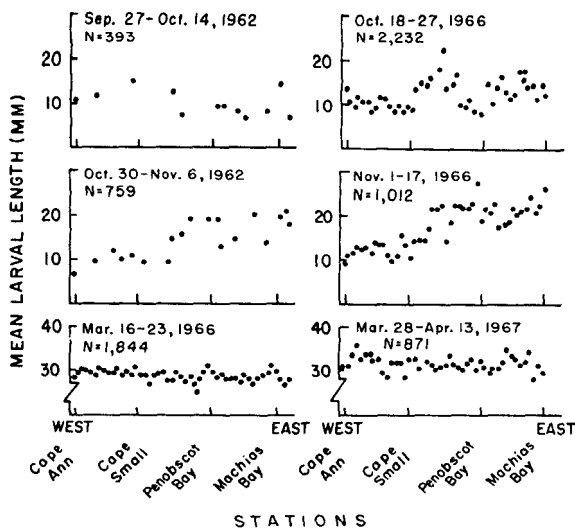


FIGURE 8.—Variations in the average length of larval herring from west to east along western coast of the Gulf of Maine.

The seasonal change in mean length (Figure 7) was influenced by the movements of larvae, their avoidance of our sampling gear, and their departure from the vicinity of our sampling stations after metamorphosis. Broods of larval herring moved shoreward in the autumn from the coastal water, but the size at which they initially entered the Boothbay area varied. This is illustrated by data from 1964 and 1965; data from 1966 were similar to those of 1965. In autumn 1964, two broods of larvae (labeled a and b in Figure 9) initially entered the Boothbay area; the more abundant had a size mode of 13 mm, the other was recently hatched and had

a size mode of 9 mm. By mid-October these two broods were of equal abundance. In November a third brood (c) was detected, during a coastal cruise, that had a modal length of 13 mm, equal to the modal length of larvae initially entering the Boothbay area. Presumably, the addition of this group in part slowed the shift in modal length to only 3 mm from mid-November to late December. These variations in size resulted from the location of the Boothbay area within an east-west coastal zone of transition for hatching time. Also, some of the larvae hatched in the eastern sector of the coast at an earlier time and were carried westward along the prevailing currents (Graham, 1970b) and then into the Boothbay area.

In autumn 1965, a single brood (d) of recently hatched larvae with a modal length of 7 mm initially entered the area. In October, this brood was still the most important contributor to the inshore area, since the modal size from a coastal cruise in October coincided with the seasonal progression of larval size within the Boothbay area. A second group (e) of recently hatched larvae entered the area in early November.

In the spring it was obvious that we were failing to catch the larger larvae and the spring peak in catch rates should have been considerably larger than that recorded for daytime tows. We assumed that this failure was due to their avoidance of our gear because we captured more of these larger larvae at night when they could not see the gear. Day and night cruises were alternated in the Boothbay area from January through April during 1965 and 1966. The size ranges of larvae captured during these cruises were the same, but the modal length was much larger for larvae captured during the night cruises. The length-frequency curves for all larvae from the day and night cruises showed two distinct modes, one at 33 mm and the other at 40 mm (Figure 10). At 36 mm the percentages of larvae in the day and night catches were identical. For larvae larger than 36 mm the percentages increased for night catches and decreased for day catches, indicating that avoidance increased progressively until the larvae grew to 40 mm. Initial nighttime catches of

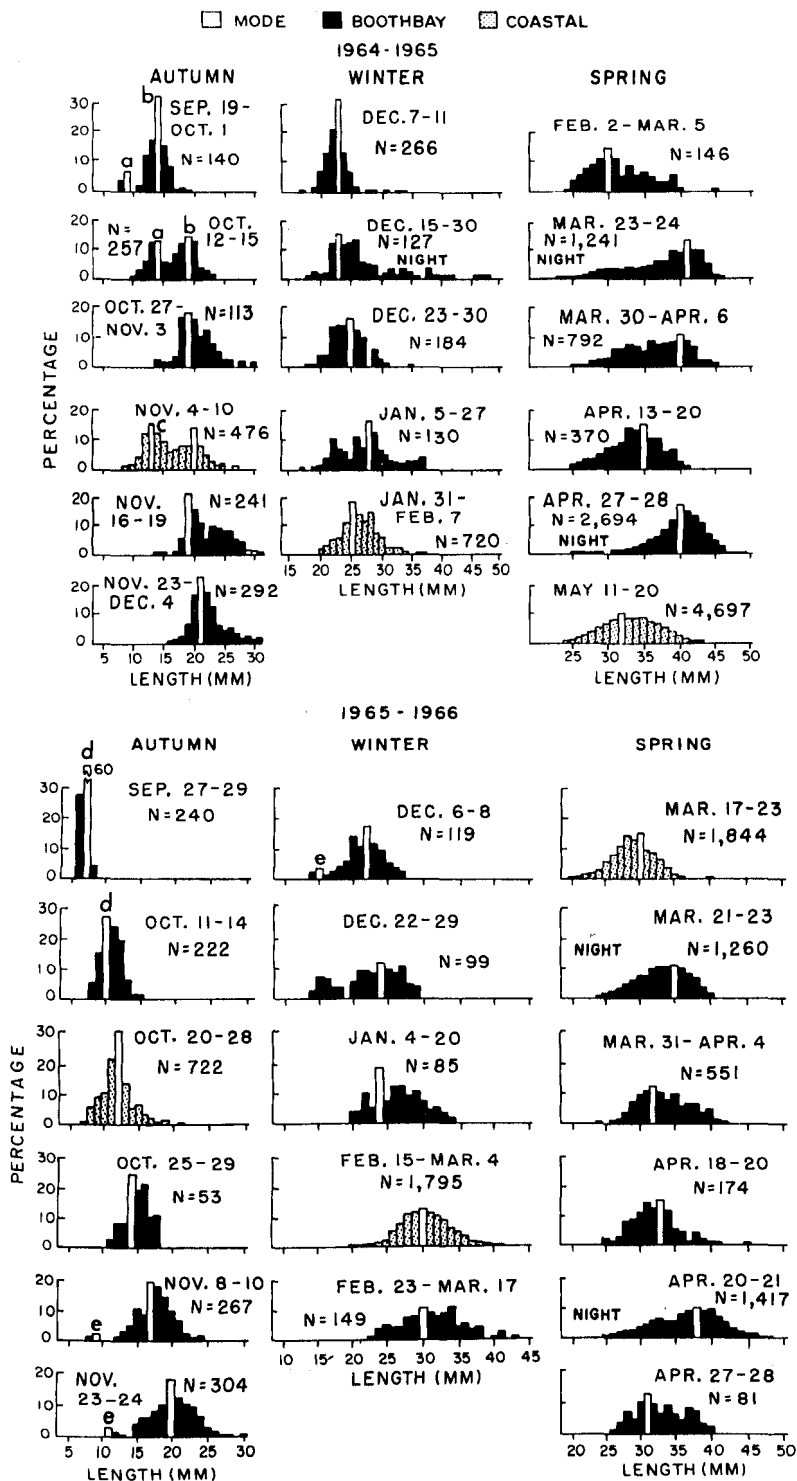


FIGURE 9.—Size distribution of larval herring during 1964-66. Only the most obvious modal lengths are indicated for the data from the Boothbay and coastal areas and those modes discussed in the text are labeled a to e.

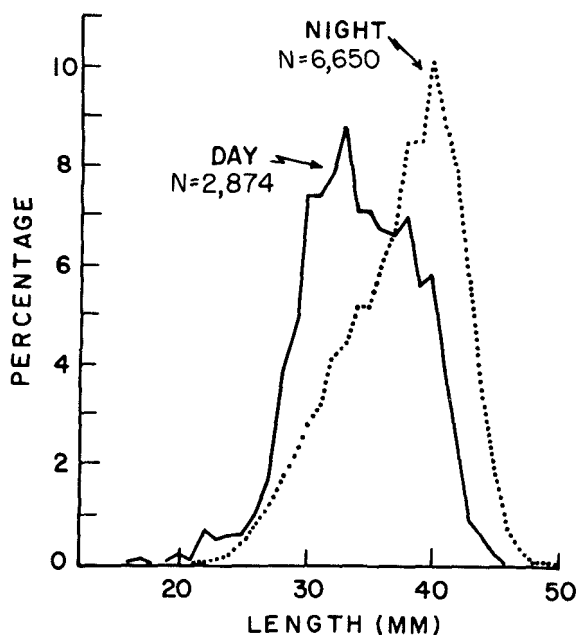


FIGURE 10.—Length-frequency curves of larvae captured in the Boothbay area at night and during the day.

those larvae larger than 36 mm occurred earlier in the year and their peak in abundance occurred later than that of larvae captured during the day (Figure 11). In 1964, losses by avoidance began in December. Failure to catch larvae began later the following year (in January) because the larvae that initially entered the Boothbay area were smaller than those that entered in 1964 (Figure 7). Catches of larvae larger than 36 mm in length in the Boothbay area were similar to those obtained with buoyed and anchored nets set in the Sheepscot estuary at night during 1966. This similarity indicated the ease with which larvae were captured at night. The buoyed nets strain water at a much lower velocity than the trawl.

In late April larvae were occasionally observed schooled in shallow coves. By late May large numbers of these fish were frequently observed in the shallow coves whereas the numbers captured at our sampling stations had declined. This change in distribution was coincident with the period of metamorphosis (about 41-50 mm SL) from larval to juvenile form. Metamor-

phosed herring were found in the Boothbay and other inshore areas but not in the outer coastal waters during the summer (Davis and Graham, 1970).

Variations in the lengths of larvae in our samples related to their shoreward movements, avoidance of gear, and departure from our sampling stations, caused discrepancies when estimating the real growth of larvae in their environment. Some estimate of growth rate may be obtained, however, from changes in modal length at certain times of the year. During 1965, the modal lengths of a single abundant group of larvae may be traced from the autumn into December. This group was not greatly influenced by mixing with other groups of different sizes and avoidance of our gear was not yet important. From late September to early December, the

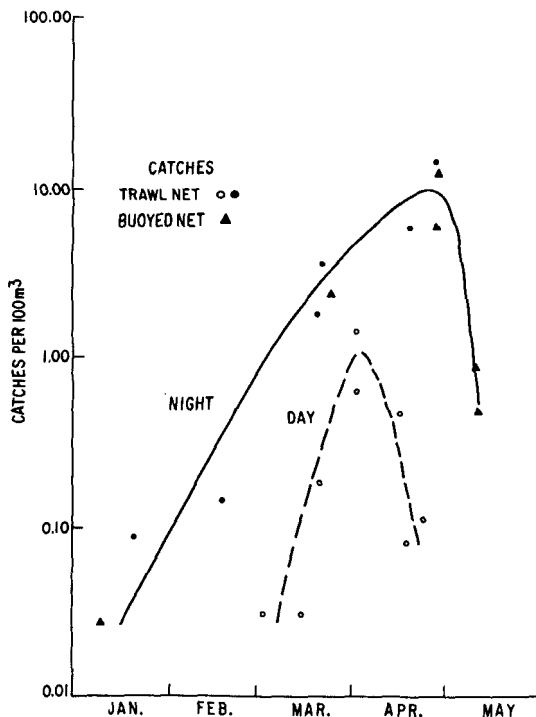


FIGURE 11.—Monthly progression of larval catches (larvae 36 mm and larger) in the Boothbay area from trawl tows at night and during the day and in the upper Sheepscot estuary from buoyed and anchored nets at night.

larvae appeared to grow about 1 mm every 5 days. Similarly, in 1964 modal lengths may be traced from late September to early November with an apparent larval growth of 1.3 mm every 5 days, but then the mode became difficult to identify.

DISCUSSION

SEASONAL CHANGES IN ABUNDANCE AND LARVAL LENGTH CAUSED BY MORTALITY

After larvae hatched and accumulated in the coastal bays and estuaries, their abundance was determined by the rate at which they died. The autumn mortality was especially severe, for the catch declined in the Boothbay area (Figure 6) despite the addition of successive broods to the area throughout the autumn. This high mortality was also indicated by the failure of length modes to persist into the winter. The number of larvae in a given mode apparently was reduced with time and coincidentally with differential growth until the larvae were too sparse in the catches to form a distinguishable mode. In 1966 the disappearance of a mode of relatively large fish from the catch caused a sharp drop in the mean larval length during November (Figure 7). Although the mean length increased either with subsequent growth of the remaining larvae or with the addition of larvae to the area, it remained below the mean lengths of the other years throughout the winter. Winter mortalities were not as high as those in the autumn. Graham and Davis (1971) determined mortalities from December to January for larvae captured in the Sheepscot estuary during 1964-67 and recently for mortalities for 1968-69. Estimates for the 6 years varied from 22% to 52% for 15-day intervals and appeared statistically reliable with the largest spread in the 0.95 fiducial interval in 1968 (27.7-36.9%), and the smallest in 1966 (22.0-22.8%).

Extensive reductions in our catch rates in the late spring occurred from avoidance of the gear by the larvae and their departure from our sampling stations. Catches at the upper estuarine

stations in the Boothbay area were larger than those at the lower and outer stations. Progressive peaks in abundance, that were present in the autumn, were absent from outer to upper estuarine stations in the spring. One explanation for the lack of progression is that the larger larvae moved landward so rapidly as to be undetected in the spring. Another and more likely explanation is that their mortality was sufficiently low to permit an accumulation of larvae at the landward extremity of their movement where numbers always greatly exceeded the number of larvae moving into the area.

Estimates of annual mortality were based on winter mortality (Graham and Davis, 1971) because measurements of total mortality during a given year were impracticable as they were influenced by larval movement in the autumn and in the spring. For most year classes, a higher winter mortality recorded in the upper end of the Sheepscot estuary coincided with a smaller maximum catch there in the subsequent spring. Also, higher winter mortalities usually coincided with a poorer condition or well-being of the larvae (Chenoweth, 1970) for the Boothbay area (Figure 12).

The causes of larval mortality along the western coast of the Gulf of Maine were not determined, but inferences were made by Chenoweth (1970) and by Sherman and Honey (1971). Essentially, they suggested that winter mortality might be related to lower lethal temperatures, inhibition of feeding by low temperatures, and a scarcity of food. Sherman (personal communication) found in recent studies that the larval guts were frequently occluded by parasites, which may cause death.

SEASONAL CHANGES IN DISTRIBUTION RELATED TO LARVAL SOURCES

After hatching, the larvae shifted their distribution from spawning areas to the coastal bays and estuaries. These destinations were apparent from our catches, but not all the sources or spawning areas were determined. The sources of larval herring in the Gulf of Maine, including the western coast, their movements from these

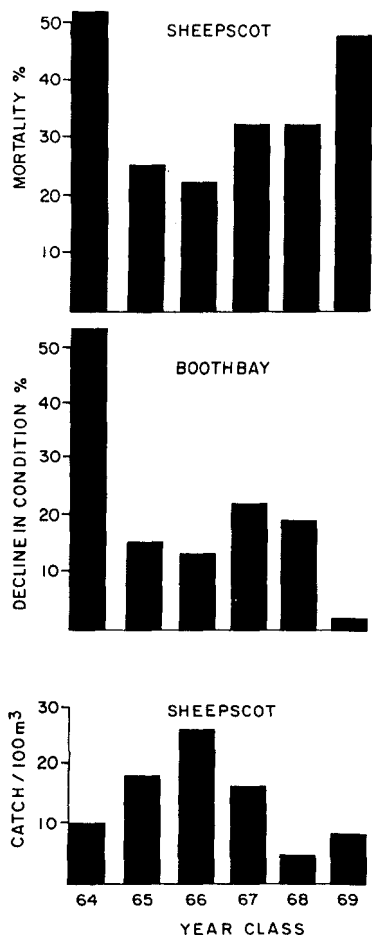


FIGURE 12.—A comparison among year classes of winter mortality of larvae in the Sheepscot estuary (upper panel), the decline in condition of larvae in the Boothbay area (center panel), and the subsequent spring catch rates in the Sheepscot (lower panel).

sources, and the resulting changes in their distributions have received attention from other investigators.

Spawning grounds of herring were located in the past by surveying the distribution of recently hatched larvae (Tibbo et al., 1958), and more recently by collecting eggs off the spawning grounds (Noskov and Zinkevich, 1967). Migrations of larvae from these grounds were traced by assuming that they were transported similarly to a particle of water. Thus, their paths

of migration from the grounds were located within the residual currents at the surface. Boyar et al. (1971) reviewed such evidence for the Georges Bank-Gulf of Maine area and decided that larvae may enter the eastern sector of our sampling area from the spawning grounds off southwestern Nova Scotia, and that some larvae from Nova Scotia may be carried along the coast of Maine as far as Cape Cod, Mass. In a concurrent paper, Iles (1971) reported on the dispersion of larvae from southwest Nova Scotia and concluded from his data that the larvae were transported into the Bay of Fundy where they were retained during the winter. Boyar et al. (1971) also suggested that larvae entered the western sector of our coast from Jeffreys Ledge, Cashes Ledge, Stellwagen Bank, and other areas collectively just offshore of the coastal sector.

The larvae from these two sources, Nova Scotia and the ledges and banks in the southwestern Gulf of Maine, possibly contributed to the coastal larval population in the spring. Such a contribution would partially explain the high catch rates obtained in the Boothbay area where larvae accumulated in the autumn and spring. The autumnal movements of larvae into the area subsided by early December. The catch in the area at that time was less than the peak catch obtained in the subsequent spring, indicating that larvae present in autumn could not account for all of the larvae found in the same area in the spring. Much of the spring catch, therefore, may be formed by emigrants. Das (1968, see footnote 2) also discovered a similar emigration by examining length-frequency distributions of larvae in the coastal area of southwest Nova Scotia. And Sameoto (1971)³ reached a similar conclusion from catches of larval herring entering St. Margaret Bay on the southeastern coast of Nova Scotia.

Another explanation for the differences in the early winter and the spring catches in our sam-

³ Sameoto, D. D. 1971. The distribution of herring (*Clupea harengus L.*) larvae along the southern coast of Nova Scotia with some observations on the ecology of herring larvae and the biomass of macrozooplankton on the Scotian Shelf. Fish. Res. Board Can., Tech. Rep. 252, 72 p.

pling areas may be deduced from the residual surface currents. In winter, the direction of these currents is usually offshore; in spring, the currents are often directed inshore. Thus, larvae swept offshore in the winter might be returned to the coast in the spring. However, we did not detect any concerted movement by the larvae offshore in the winter and suspect that the assumption that larvae are transported similarly to a particle of water is often an oversimplification. The factors controlling the movement and retention of the larvae in shoal water must be investigated to understand the possibilities of their transport.

ANNUAL CHANGES IN ABUNDANCE AND THE FISHERY

The goal of this research was to choose an estimate of larval abundance or its correlate that could be used to predict the annual recruitment of immature 2-year-old herring to the sardine fishery of the western coast of the Gulf of Maine. Three different types of estimates were chosen: (1) winter mortality, (2) condition in the winter, and (3) maximum abundance in the spring. Sampling should continue over a number of years to determine whether the relations between the three measures have substance and whether any one or all of them are pertinent to predicting the abundance of 2-year-old herring.

A tentative comparison between the percentage of 2-year-old fish taken in the fishery with the percentage of winter mortality of the corresponding year class during 1964-68 is shown in Figure 13. Years of low mortality were usually related to subsequent greater percentage of 2-year-old fish in the fishery.

Estimates of winter condition are important because they provide an insight as to the cause of larval mortality. Because winter condition correlates with winter mortality, larval deaths are probably caused by debilitating factors such as disease, starvation, or parasitism. But, lack of agreement during 1969 (Figure 12) would involve other factors as well, such as predation or sudden and transient effects of man's activities within the coastal environment.

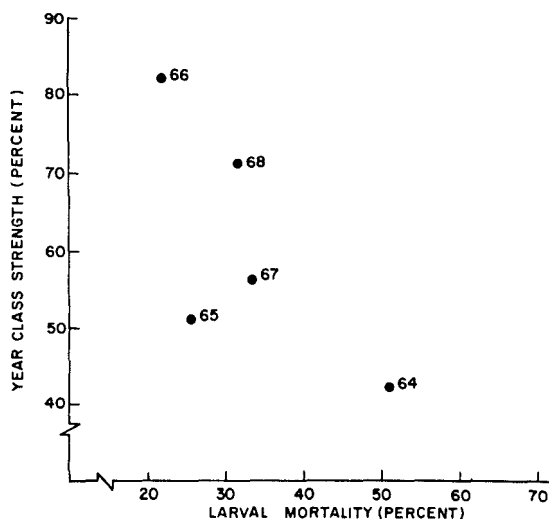


FIGURE 13.—Comparison between the percentage of 2-year-old herring captured in the Maine sardine fishery and the winter larval mortality for a given year class. Age composition of the fishery was determined by John E. Watson (personal communication). The catch also includes fish from the adjacent Canadian coast.

Estimates of abundance in the spring are necessary as well as winter mortality estimates because the number of larvae surviving until spring theoretically depends upon the initial number of larvae present by the end of autumn. During each of the years in which winter mortality was estimated in this study, the autumnal abundance was reduced to approximately the same level by early winter. During years of very successful hatching, the autumn mortality might not be sufficient to reduce the number of larvae to a level common to that of previous years. The subsequent spring abundance would then be determined by the initial number of larvae present in early winter as well as the winter mortality. The estimates of spring abundance in the Boothbay area and in the coastal area between Cape Small and Penobscot Bay (Figure 14) did not agree with the estimates obtained with buoyed and anchored nets in the Sheepscot for year classes 1964-65 (Figure 12, bottom panel). We do not understand the reason for this difference.

To date, monitoring of the winter mortality

and condition and spring abundance of larvae has been largely confined to the Boothbay area; the possibility of extending monitoring to other areas of the coast is being investigated. Nevertheless, events in the ecology of the larvae in the Boothbay area could represent those of the entire coast of the Gulf. Seasonal changes in larval abundance are similar along the coast and are comparable to those in the coastal area off southwest Nova Scotia (Das, 1968, see footnote 2) and on Georges Bank (Boyar et al., 1971). Yearly changes in oceanic conditions along the coast and in the offshore Gulf of Maine are also related (Colton, 1968). Further correlation between ecological events in the Boothbay area and those in other areas of the Gulf, at least adjacent areas, is evidenced by the agreement of the winter mortality estimates obtained in the Sheepscot and the subsequent spring abundance there. Larvae captured in the spring include emigrants from areas other than Boothbay. Correct forecasts of a poor fishery, to date, coincided with poor recruitment to the fishery; unfortunately, forecasts have not been made during years of good recruitment in the western sector.

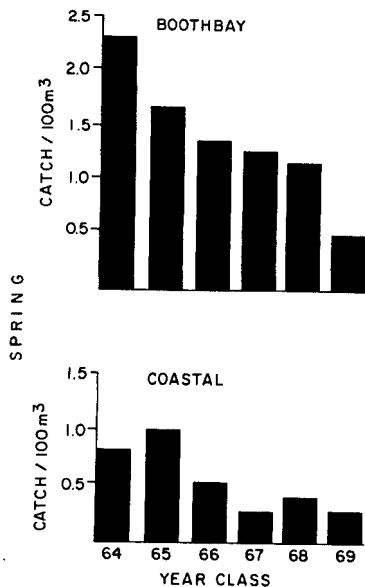


FIGURE 14.—Peak catches for larval herring in the spring among year classes 1964-69; in the coastal area between Cape Small and Penobscot Bay and in the Boothbay area.

SUMMARY OF ABUNDANCE AND DISTRIBUTION

The abundance and distribution of larval herring along the western coast of the Gulf of Maine is determined by their movements and mortality. Two inshore movements, one in the autumn and the second in the spring, are separated by a period of larval dispersal. Larvae hatch along the coast in autumn and penetrate the bays and estuaries. Their inshore movement decreases by early winter and in midwinter they disperse; at this time concentrations of larvae are infrequent inshore and along the coast. A second shoreward movement begins with the advent of spring. Larvae which hatched the previous autumn along the coast, and probably some which hatched beyond our sampling area, aggregate when making this shoreward movement. The inshore movement is completed by the end of spring when the majority of the larvae have assumed their adult form.

Mortality during the inshore movement in the autumn is very high. Although it is lower in the winter, mortality during this season may determine the abundance of larvae in the spring because the numbers are reduced by early winter to a relatively common level each year. The lower winter mortality may be related to the dispersal of the often weakened larvae; dispersal would reduce intraspecific competition for food and space. The lowest mortality occurs in the spring when the larvae are in good condition as shown by their ability to avoid high-speed trawls with large mouth openings.

The movement of the larvae shoreward within the complex currents of the coast is a striking feature of their coastal ecology.

LITERATURE CITED

- ANTHONY, V. C., AND H. C. BOYAR.
1968. Comparison of meristic characters of adult Atlantic herring from the Gulf of Maine and adjacent waters. *Int. Comm. Northwest Atl. Fish., Res. Bull.* 5:91-98.
- BIGELOW, H. B., AND W. W. WELSH.
1925. Fishes of the Gulf of Maine. *Bull. U.S. Bur. Fish.* 40 (Part I), 567 p.

- BOYAR, H. C.
1968. Age, length, and gonadal stages of herring from Georges Bank and the Gulf of Maine. Int. Comm. Northwest Atl. Fish., Res. Bull. 5:49-61.
- BOYAR, H. C., R. R. MARAK, F. E. PERKINS, AND R. A. CLIFFORD.
1971. Seasonal distribution of larval herring, *Clupea harengus harengus* Linnaeus, in Georges Bank-Gulf of Maine area, 1962-70. Int. Comm. Northwest Atl. Fish., Res. Doc. 71/100, 11 p.
- BUMPUS, D. F., AND L. M. LAUZIER.
1965. Surface circulation on the continental shelf off eastern North America between Newfoundland and Florida. Ser. Atlas Mar. Environ. Am. Geogr. Soc. Folio 7, 8 plates, [4] p.
- CHENOWETH, S. B.
1970. Seasonal variations in condition of larval herring in Boothbay area of the Maine coast. J. Fish. Res. Board Can. 27:1875-1879.
- COLTON, J. B., JR.
1968. Recent trends in subsurface temperatures in the Gulf of Maine and contiguous waters. J. Fish. Res. Board Can. 25:2427-2437.
- COLTON, J. B., JR., AND R. F. TEMPLE.
1961. The enigma of Georges Bank spawning. Limnol. Oceanogr. 6:280-291.
- DAVIS, C. W., AND J. J. GRAHAM.
1970. Brit herring along Maine's coast. Commer. Fish. Rev. 32(5):32-35.
- GEHRINGER, J. W., AND W. ARON.
1968. Field techniques. In D. J. Tranter (editor), Reviews on zooplankton sampling methods, p. 87-104. UNESCO Monogr. Oceanogr. Methodol. 2(Part 1).
- GOODE, G. B.
1884. The herring tribe. The herring—*Clupea harengus*. In G. B. Goode and associates, The fisheries and fishery industries of the United States. Section I. Natural history of useful aquatic animals, p. 549-568. Gov. Print. Off., Wash. [D.C.]
- GRAHAM, J. J.
1970a. Temperature, salinity, and transparency observations, coastal Gulf of Maine, 1962-65. U.S. Fish Wildl. Serv., Data Rep. 42, 43 p.
1970b. Coastal currents of the western Gulf of Maine. Int. Comm. Northwest Atl. Fish., Res. Bull. 7:19-31.
- GRAHAM, J. J., AND H. C. BOYAR.
1965. Ecology of herring larvae in the coastal waters of Maine. Int. Comm. Northwest Atl. Fish., Spec. Publ. 6:625-634.
- GRAHAM, J. J., AND C. W. DAVIS.
1971. Estimates of mortality and year-class strength of larval herring in western Maine, 1964-67. Cons. Perm. Int. Explor. Mer, Rapp. P.-V. Réun. 160:147-152.
- GRAHAM, J. J., AND G. B. VAUGHAN.
1966. A new depressor design. Limnol. Oceanogr. 11:130-135.
- GRAHAM, J. J., AND P. M. W. VENNO.
1968. Sampling larval herring from tidewaters with buoyed and anchored nets. J. Fish. Res. Board Can. 25:1169-1179.
- ILES, T. D.
1971. The retention inside the Bay of Fundy of herring larvae spawned off the southwest coast of Nova Scotia. Int. Comm. Northwest Atl. Fish., Res. Doc. 71/98, 7 p.
- NOSKOV, A. S., AND V. N. ZINKEVICH.
1967. Abundance and mortality of herring, *Clupea harengus* Linnaeus, on Georges Bank according to the results of egg calculation in spawning areas in 1964-66. Int. Comm. Northwest Atl. Fish., Res. Doc. 67/98, 16 p.
- RIDGWAY, G. J., R. D. LEWIS, AND S. W. SHERBURNE.
1969. Serological and biochemical studies of herring populations in the Gulf of Maine. Int. Counc. Explor. Sea C. M. 1969/24, 13 p.
- SHERMAN, K.
1970. Seasonal and areal distribution of zooplankton in coastal waters of the Gulf of Maine, 1967 and 1968. U.S. Fish Wildl. Serv., Spec. Sci. Rep. Fish. 594, 8 p.
- SHERMAN, K., AND K. A. HONEY.
1971. Seasonal variations in the food of larval herring in coastal waters of central Maine. Cons. Perm. Int. Explor. Mer, Rapp. P.-V. Réun. 160:121-124.
- TIBBO, S. N., J. E. H. LEGARÉ, L. W. SCATTERGOOD, AND R. F. TEMPLE.
1958. On the occurrence and distribution of larval herring (*Clupea harengus* L.) in the Bay of Fundy and the Gulf of Maine. J. Fish. Res. Board Can. 15:1451-1469.