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Abundance and Mortality Estimates for Sea Herring (*Clupea harengus* L.) Larvae Spawned in the Georges Bank-Nantucket Shoals Area, 1971-1978 Seasons, in Relation to Spawning Stock and Recruitment

by

R. G. Lough, G. R. Bolz, M. R. Pennington, and M. D. Grosslein
NOAA, National Marine Fisheries Service
Northeast Fisheries Center
Woods Hole, Massachusetts 02543

INTRODUCTION

Surveys of Atlantic larval herring (Clupea harengus harengus L.) have been conducted in the Georges Bank - Gulf of Maine region since the 1950's to provide information regarding the seasonality of spawning, spawning grounds, and relative size and possible intermixing of populations in the area (Tibbo et al. 1958; Tibbo and Legaré 1960; Colton et al. 1961; Marak and Colton 1961; Marak et al. 1962a,b). Spawning occurs predominantly in the autumn in the shoal areas of Southwestern Scotian Shelf (Das 1968), Western Gulf of Maine, and Georges Bank (Graham et al. 1972). Boyar et al. (1973) have summarized the seasonal distribution of larval herring in the Georges Bank - Gulf of Maine region from 1962 to 1970 and concluded that larvae originating from the three spawning areas remained discrete throughout the larval period due to restrictive circulation patterns.

With the development of the herring fishery on Georges Bank by foreign fleets in the 1960's, the herring catch increased dramatically until 1968 and then rapidly declined thereafter to virtually zero in 1977, in spite of the strong 1970 year-class (Anthony and Waring 1978). Recruitment fluctuations of sea herring stocks are believed to be caused chiefly by differential mortality during the larval period, as evidence shows no strong relationship between recruitment and spawning stock over a wide range of spawning stock size, and the fact that the size of a year-class appears to be fixed within limits by the time they are juveniles (Anthony and Waring 1978). Interest in the conservation of the stock and the general belief in the hypothesis that success of a year-class is controlled by factors operating during the larval period led the International Commission for the Northwest Atlantic Fisheries (ICNAF) to develop a major cooperative research program on the early life history of the autumn spawning sea herring in the Georges Bank - Gulf of Maine region. ICNAF larval herring surveys began in autumn 1971 and were designed to measure major variations in larval production, dispersal, mortality and growth in the first 6 months of life with the long-term objective of identifying mechanisms controlling larval survival, or at least environmental conditions associated with large and small year-classes. The Georges Bank - Nantucket Shoals area represents our most complete and intensive time series of data over the 8 seasons studied. In this paper, abundance and mortality estimates are presented in relation to potential egg production of the spawning stock and available recruitment indices for the 1971-1978 spawning seasons, Georges Bank - Nantucket Shoals area. The results here are based primarily on the 0.333-mm mesh samples sorted in Poland using standard protocols. Analyses made using only the 0.505-mm mesh samples, which where sorted by each participating country, have been reported previously by Lough et al. (1979).

METHODS

Field Sampling

A summary of the 39 larval herring surveys and sample mesh size used in this study is given in Table 1. A station plot and typical cruise track of the Georges Bank - Nantucket Shoals area emphasized since 1974 is shown in Figure 1. When the ICNAF larval herring surveys were initiated in 1971, the approach was to cover the entire Georges Bank - Gulf of Maine area with a standard grid of sampling stations 24-32 km (15-20 miles) apart at least once a month from September through December. At each station a 6.5 km/hr (3.5-knot) double-oblique tow was made using a 61-cm bongo sampler (0.505- and 0.333-mm mesh) (Posgay and Marak 1980). The gear was deployed at 50 m/min to a maximum depth of 200 m or to within 5 m of the bottom in shoaler areas. The rate of retrieval was at 20 m/min up to 40 m depth and changed to a step-oblique profile sampling 20 2-m steps 1 min each. On ALBATROSS IV 71-07, the net was retrieved continuously at 10 m/min in the upper 40 m. Beginning in 1972 the tow profile was changed to its present state where the maximum depth of tow was to 100 m and retrieved continuously at the rate of 10 m/min.

In February 1974 the USA began a series of February surveys to examine the overwinter picture. In June 1974 the newly formed ICNAF Environmental Working Group recommended more intensive studies of factors controlling the recruitment process. Small bongo samplers (20 cm) with fine mesh nets were added to the 61-cm bongo array beginning in autumn 1974. Since the 1975 season, sampling effort has concentrated on the Georges Bank - Nantucket Shoals area alone (Figure 1) so that more emphasis could be given to studying circulation of this area with concurrent studies of primary production. Thereafter, sampling was expanded to include a finer grid of plankton stations in areas of heavy spawning aggregations, more complete hydrographic coverage, and nutrients, chlorophyll, and primary production when possible. More detailed information concerning cruise and station data as well as the sampling methods can be found in Lough and Bolz (1979).

Sample Processing

All available 0.333-mm mesh samples from the time series were sorted at the Polish Sorting Center (Morski Instytut Rybacki), Szczecin, Poland, for total ichthyoplankton. In most cases all herring larvae were removed from the samples except in those few instances where extremely high densities required subsampling. The standard length (SL) of up to 100 larvae per sample was measured to the nearest 0.1 mm to represent the sample length-frequency distribution. Discrepancies in the total number of standardized herring larvae between the 0.333-mm and 0.505-mm mesh samples have been noted by Bolz (1980). For this study, 0.505-mm mesh data were substituted for the 0.333-mm data in 12 of 39 surveys to represent the best possible data base (Table 1).

Larval Abundance and Mortality Estimates

Larval herring station catches from each survey were first standardized to number per m^2 sea surface area by 1-mm length classes according to the formula

$$N = \frac{CZ}{V} \tag{1}$$

where, N = number of larvae per square meter sea surface by station

C = catch of larvae

Z = depth of tow in meters

V = volume filtered by net in cubic meters.

The mean density of larvae from each survey within the Georges Bank - Nantucket Shoals spawning area was estimated using the delta (Δ) - distribution (Aitchison and Brown 1957), which has been found by Pennington (1980) to be an efficient estimation of the mean density for egg and larval surveys containing a proportion of zero catches. Unbiased estimators of the arithmetic mean (c) and variance of the Δ-distribution given by Pennington (1980) are:

$$c = \left(\frac{m}{n}\right) e^{\bar{y}} X_m \left(\tfrac{1}{2} s^2\right) \qquad (2)$$

and

$$\mathrm{var}\,(c) = \frac{m}{n} e^{2\bar{y}} \left[\frac{m}{n} X_m^2 \left(\frac{s^2}{2}\right) - \left(\frac{m-1}{n-1}\right) X_m \left(\frac{m-2}{m-1} s^2\right)\right] \qquad (3)$$

where, n = number of tows

m = number of non-zero catches

$\bar{y}$ = sample mean of $\log_e$ (no. larvae/m^2) for non-zero catches

s^2= sample variance of the log values

$X_m(t)$ = is a function defined by an infinite series which can be found in the above references.

Confidence intervals can be generated by assuming c (or weighted sum of the c's when estimating totals) is approximately normally distributed with standard error equal to $\sqrt{\mathrm{var}\ (c)}$. When the proportion of zeros is zero, the Δ-distribution is lognormal and the above estimators may still be used.

Before seasonal abundance estimates were made, the data was examined by cruise and season for two sources of sampling error: 1) night-day avoidance of the nets and 2) extrusion of small larvae through the net mesh. A summary plot of the combined data from 35 surveys (1971-77) of larval herring night and day mean abundance (c) by 1-mm length classes is shown in Figure 2. The peak in abundance of recently-hatched larvae begins with the 7-mm length classes and declines exponentially with length so that few larvae are caught larger than 24 mm. The mean length of larvae at hatch is 5.66 mm (Lough et al. 1980). The mean night and day abundance of larvae were not significantly different for all length classes, although more 7-mm larvae were caught by day than night, and there is a definite trend of more larvae caught by night than day for individuals greater than 12 mm. The average percentage of hauls made by night for all seasons was 55.3% (2.1 SD). Night to day abundance ratios of the same data is given in Figure 3. The ratios appear to be near unity for the 7-12-mm length classes and then increase in a linear fashion up to a ratio of ca. 5 at about 31 mm, after which the ratios show extreme variability and appear to decline after 36 mm. These ratios indicate that avoidance of the net began after ca. 12 mm and became a serious problem which we could not correct for easily after ca. 30 mm.

Minimum lengths for complete retention of herring larvae caught on ICNAF surveys in the 0.505-mm and 0.333-mm mesh nets were estimated by Colton et al. (1980) to be 12.0 mm and 7.5 mm, respectively. In our study a station by station comparison of abundance of small herring larvae (>8 mm) did not indicate any significant difference in the mean abundance between the two mesh sizes in 13 of the surveys examined, so that we do not feel that extrusion is significant for larvae 7 mm and larger. A possible explanation for the fact that more small larvae (esp. 7-mm length class) were caught by day than night is that the recently-hatched larvae are still quite localized and there are proportionately more daylight hours for collecting larvae early in the season than later. Besides being quite localized over the spawning beds at hatch, recently-hatched larvae in the 6-mm length class may be undersampled because they have been observed to reside during the first few days within the egg beds or just below our maximum depth of sampling (Caddy and Iles 1973; Cooper et al. 1975).

A simple regression line was fitted to the 13- to 30-mm night/day ratios (Y) (drawn in Figure 3), which results in the equation:

$$Y = 0.213\ L - 1.805 \qquad (4)$$

$$(r = 0.90)$$

where, L = standard length of larvae in millimeters.

All catches of larvae in the 13-30-mm length classes collected by day hauls were adjusted by equation (4) so that they were comparable to night catches. Thus, in this study the 7-30-mm length classes are considered to be fully vulnerable to the net.

Seasonal abundance estimates using night-day adjusted catches were made now by the expanded day and area method of Sette and Ahlstrom (1948). For each survey within a season the mean density (c) of larvae was estimated for each 1-mm length class within the 7-30-mm fully vulnerable size classes and multiplied by the number of days (D) represented by the survey and by the total Georges Bank-Nantucket Shoals area encompassed by the study ($99.75 \times 10^9 m^2$). Survey abundance estimates are summed by 1-mm length classes to give the total seasonal abundance estimates.

Length-specific mortality rates were estimated for each season by a simple exponential regression of abundance on length for the 7-30-mm length classes;

$$A_L = A_o e^{-ZL} \quad (5)$$

where, A_L = abundance of larvae at length L in millimeters

A_o = abundance of larvae at initial length zero

Z = instantaneous rate of apparent mortality per unit length

L = standard length of larvae in millimeters.

An estimate of the initial abundance of larvae extrapolated to 5.66 mm, the length at hatching, was estimated from each regression and the 95% confidence limits based on the methods described in Draper and Smith (1966, p. 22).

A consequence of using equation (5) is that the instantaneous rate of mortality, Z, with respect to length is assumed constant. One generating mechanism for such a simple model would be that $100e^{-Z\varepsilon}$% of the larvae on average obtain sufficient food to grow from length L to $L+\varepsilon$; larvae that do not grow, die. Whether or not there is any biological validity in using equation (5) is debatable, but it appears adequate for the purpose of estimating the apparent average seasonal mortality of field larvae as a function of length. Ideally the initial abundance of larvae at hatching should be made using only the smallest length classes since the mortality rate varies over the season; however, sampling of the smallest larvae on these surveys was not adequate for this purpose.

Mortality is best described as a function of age. In order to estimate mortality as a function of time, equation (5) is coupled with a Gompertz decaying exponential model describing larval herring growth in length from hatch (5.66 mm) to an upper asymtotic limit of 30.895 mm at 175 days (Lough et al. 1980):

$$L = 30.895 \exp\left[-1.698 \exp\left(-0.026x\right)\right]. \quad (6)$$

where, L = standard length of larvae in millimeters

x = age in days.

Then,

$$\frac{dA_L}{dx} = \frac{dA_L}{dL} \cdot \frac{dL}{dx}$$

and hence from equation (5),

$$\frac{dA_L}{dx} = -ZA_L \frac{dL}{dx} \quad . \quad (7)$$

Thus, for example, combining the regression equation of larval abundance on length for the 1974 season (Z = 0.197, see Figure 6d) and equation (6), the estimated instantaneous mortality rate with respect to age is given by the equation:

$$M_x = \frac{-dA_L}{A_L dx} = -0.27 \exp\,[-1.70 \exp(-0.026t) -0.026t]. \qquad (8)$$

A plot of the change in the instantaneous mortality rate (M_x) with respect to age of herring larvae from equation (8), for the 1974 season, is shown in Figure 4. For each of the spawning seasons, 1971-1978, average instantaneous mortality rates (M_x) were estimated over 0-100 days (representing the autumn period), 100-150 days (winter period), and 0-150 days (autumn-winter seasonal average). In all cases there is a peak in mortality (M_x) for larvae approximately 20-days old due to the functional form of the growth model which has an inflection point at 20.28 days. If the growth curve is sigmoidal shaped, then the instantaneous growth (dL/dx) will have a maximum, and since the rate dA_L/A_L is assumed to be constant, the mortality rate estimates, M_x, from equation (7) also will have a maximum. Although the precise shape of the mortality curve (M_x) may be an artifact of the model, it does appear to provide a reasonable estimate of the level of age-specific mortality over a spawning season. The model does not permit the discrimination of variable mortality rates within a spawning season, such as between autumn and winter months by the methods used here.

RESULTS

Time of Spawning and Distribution of Larvae

Survey coverage of the Georges Bank - Nantucket Shoals standard stations where major larval herring concentrations were located was virtually complete for the autumn season of 1971-1972 and for the autumn-winter seasons of 1973-1978 (Table 1). Sea herring, which have demersal eggs, typically spawn on gravelly or red algal substrate at a mean depth of 40 m or less, in waters characterized by strong mixing processes (Drapeau 1973, Cooper et al. 1975). Hatching of larvae has been observed in the field by Cooper et al. (1975) to occur 8-9 days after spawning at a temperature of ca. 10°C. One can define major spawning sites and the general shape of the spawning curve for each season using the cruise abundance estimates of larvae <10 mm SL (mean length class of 6 mm at hatching) to represent the recently-hatched larvae. Within a given season the mean cruise abundance indices almost invariably show a systematic progression from low to high to low numbers during the September-

December period which is consistent with a concentrated spawning in one time and place (Lough et al. 1979). In Table 2, the timing and length of the spawning (hatching) season and the percentage of recently-hatched larvae (<10 mm SL) collected on the spawning grounds of Georges Bank and Nantucket Shoals are estimated for each season from 1971 to 1978. A spawning curve for the combined Georges Bank - Nantucket Shoals area approximates a lognormal distribution curve with a weighted middate of the time series lying between the latter half October and first part of November. Spawning occurs progressively later in the season from north to south in the study area. The northeastern part of Georges Bank is a major spawning area where recently-hatched larvae normally attain maximum abundance by mid-to-late October. The Nantucket Shoals spawn typically hatch 1-2 weeks later than those on Georges Bank and peak in abundance by late October-early November. Spawning (hatching) began in early September at the start of the time series for the 1971-1973 seasons, delayed apparently until the end of September for the 1974 and 1975 seasons, and delayed further until as late as mid-October for the 1976-1978 seasons. The end of the spawning season in late December also may have come 1-2 weeks earlier in mid-December since the 1976 season, but it remained essentially the same during all years except for the unusual 1976 season. As will be noted in the data presented later in the paper, production of larvae was extremely low in 1976 and thereafter. In effect, over the time series, the major change observed in the spawning curve of herring was a delay in the onset of spawning from September to October, contracting the length of the season from about 4 to 2-3 months in duration. Spawning usually occurs predominantly in one area or the other. The main spawning concentrations were located in the Georges Bank area in 1971, 1973, and 1974, and in the Nantucket Shoals area in 1972, and 1975-1978

In Figure 5 a sample plot from the 1974 season shows a fairly typical sequence of the spread of larvae from spawning areas on Georges Bank and Nantucket Shoals from an initial survey in September through the 4th survey in December. The main concentrations of larvae followed from the spawning areas (designated by larvae less than 10 mm through succeeding 5-mm length classes) is based upon the fact that larval herring grow in length ca. 5 mm per month which is consistent with the timing of the surveys which were conducted at approximately monthly intervals. Peculiarities in the spread and dispersal of larvae for each of the seasons will not be discussed in any detail in this paper but some important generalizations will be noted here. Larvae originating from the Georges Bank and

Nantucket Shoals spawning areas disperse rapidly over the shoal areas reaching the maximum extent of their distribution by late November-December after which the size of the populations begin to reduce dramatically. During the late autumn and winter months a southerly flow of surface waters is suggested on Georges Bank with a westerly component across the Great South Channel (Bumpus 1976). Larvae from the northeastern Georges Bank spawning area typically disperse to the southwest across Georges at the rate of 1-8 miles per day and intermix with larvae originating from the Nantucket Shoals spawning area. Larger larvae can be found at times off the Bank in the central Gulf of Maine and in lobe-like distributions extending off the Northeast Peak and in the Slope Water south of Georges but, generally, the bulk of the larval population is found throughout the season within the 100-m contour, the shoal waters in which they originated. There is little evidence from these data to suggest any cross transport of larvae between Georges Bank and Browns Bank, nor between coastal western Gulf of Maine and Nantucket Shoals, at least as larvae during their first 6 months of life. The Georges Bank - Nantucket Shoals area represents our most complete and intensive time series of data; however, the shoal waters (<25 m) of Nantucket Shoals have not been sampled adequately in all years and this area may be an important nursery ground for larvae as well as juveniles. Larvae produced in the coastal areas near shore apparently migrate into the estuaries and embayments during the autumn and remain there through the winter (Graham and Davis, 1971, Graham et al. 1972). Also, at times the surveys have not been able to extend their coverage far enough off the southern edge of the shelf and adequately survey the western limit of Southern New England waters to encompass the most extreme reaches of the larval populations through the course of their early life. The extent of the underestimation of larval abundance due to incomplete sampling coverage is not known but we believe that it would not materially effect the estimates of mortality derived by the methods used in this paper.

Abundance and Mortality Estimates

The seasonal mean haul density of larvae (c), standard error of c, and expanded abundance estimates (A_L) by 1-mm length classes (7-30 mm) are given in the APPENDIX for the 1971-1978 seasons. These same seasonal abundance estimates are depicted in Figures 6a-h along with the exponential curve-fit extrapolated back to an initial hatching length of 5.66 mm. Table 3 summarizes the initial abundance estimates with 95% confidence limits, length-specific (Z_L) and age-specific

(M_x) mortality rates for the 1971-1978 seasons. These initial larval abundance estimates appear to be reasonable based on previous work (Lough et al. 1979) and show production of larvae in the Georges Bank - Nantucket Shoals area to have been relatively high in 1973 and 1974 (79-121 x 10^{12}), intermediate in 1971, 1972, and 1975 (20-43 x 10^{12}), low in 1977 and 1978 (2-5 x 10^{12}), and extremely low in 1976 (<1 x 10^{12}). The lower and upper 95% confidence limits for these initial estimates lie within the range of approximately half to double the predicted value which is reasonable for these kind of data (Saville 1964). All correlation coefficients for the exponential regressions of abundance on length ranged between 0.815 and 0.973, and were significantly different from zero. The predicted initial abundance estimates at 5.66 mm were higher than the actual abundance of larvae caught in the 7-9 mm-length classes for the years 1971-73, 1977, and 1978 by a factor of ca. 2-4; the 1975 year predicted estimate was lower by a factor of ca. 2, and the 1974 and 1976 predicted initial estimates were most nearly equal to the actual abundance levels of the 7-9-mm length classes. One must also bear in mind that there was no February survey conducted during the 1971 and 1972 seasons as in more recent years; the effect of which if present, usually tends to decrease the slope of the fitted exponential curve and consequently lower the initial abundance estimate.

The instantaneous rate of decline in abundance with length (Z_L), or length-specific mortality rate, ranged from a low of 0.135 per mm length in 1976 to a high of 0.295 in 1978 with an average rate of 0.210 over the 8-years studied. The average mortality rates over the 8 seasons can be grouped into similar levels as follows: the 1975 and 1976 seasons had the lowest levels of mortality (0.135-0.165), the 1973, 1974, and 1977 seasons were intermediate (0.189-0.210), the 1971 and 1972 seasons high (0.246), and the 1978 season was the highest of all seasons (0.295). In terms of age-specific average mortality (M_x) over 150 days, the average instantaneous mortality rates were 0.022-0.027 (2.2-2.7% per day) in 1975 and 1976; 0.030-0.034 (3.0-3.4% per day) in 1973, 1974, and 1977; 0.040 (3.9% per day) in 1971 and 1972; and 0.047 (4.6% per day) in 1978. The combined 8-year overall average age-specific mortality rate for the first 100 days representing the autumn period was 0.045 (4.4% per day), for 100-150 days, the winter period, 0.011 (1.1% per day), and for 0-150 days, the autumn-winter period, 0.034 (3.3% per day).

Potential Egg Production from Larval and VPA Assessment Data

Another important calculation from the larval herring surveys is the comparison of potential egg production derived on one hand from the larval data and on the other, from the virtual population assessments (VPA) of adult spawning stock size. The methodology and assumptions used to derive the independent egg-productions estimates can be investigated for any discrepancy observed by a comparison of the two. One might be able to infer the causes of mortality such as the magnitude of egg-mortality between years and areas.

A comparison is made in Table 4 of the potential egg production derived by Anthony and Waring (1980) from the most recent Georges Bank VPA herring stock estimate and derived from the larval initial abundance estimates in this paper for the 1971-1978 year-classes. Sea herring in the Georges Bank and Gulf of Maine region generally became sexually mature by late summer of their third or fourth year, and Boyar (1968) found that variable (6-62%) proportions of herring matured at age 3 and 92% maturity at age 4 on Georges Bank for the 1960-1965 year-classes. With the decline of the older fish in the population, more of the herring in the Georges Bank stock are believed to be maturing at age 3 and age 4. Anthony and Waring (1980) estimated that after 1970, 93% of age 3 and all age 4 herring were mature on Georges Bank. Two estimates of egg production are provided by them: one based on a scaled fecundity which assumes an inverse relationship between population abundance and fecundity, and the second, a constant fecundity based solely on the data provided by Perkins and Anthony (1969) for 1963-64. Both fecundity estimates are similar with the scaled fecundity estimate being slightly greater than the constant fecundity estimate. Severe fishing restrictions were in effect during the 1976 season and there was no herring fishing allowed on Georges Bank after the extremely low 1976 season.

The seasonal estimate of eggs produced from the larval data was considered equivalent to the estimated initial abundance estimates at hatching (5.66 mm). These estimates are based upon the assumption of a constant length-specific mortality rate over the season and extrapolated back from the 7-mm length class to initial hatching size. Newly-hatched yolksac larvae have been observed by divers (Caddy and Iles 1973, Cooper et al. 1975) to stay within a meter of the bottom or within the substrate for 1-3 days after hatching. Plankton gear used on the larval herring surveys only sampled to within 5 m of the bottom and therefore there is little direct evidence on the magnitude of natural mortality during the first few days after hatching. Also, no egg bed mortality correction factor was applied to the initial larval abundance estimates as hatching success is believed to be near 100% and predation on the egg beds could vary significantly by an undetermined amount. Although herring eggs may be deposited in layers up to 5-cm thick, observations in this region indicate egg mortality from spawning through hatching may be less than 1%, excluding predation (Pankratov and Sigajev) 1973, Cooper et al. 1975). Survival is believed to be greater for eggs deposited in thin layers, such as on algal-covered substrate, than in multilayered beds. Along the nearshore area, red algae provide a substrate in waters less than 40 m (McKenzie 1964, Cooper et al. 1975). Egg predation by various species of fish and invertebrates was estimated to be 8% within 1-2 days after egg deposition on Georges Bank in 1970 (Caddy and Iles 1973). With hatching occurring 8-9 days after spawning (10°C), predation could possibly account for 30-70% of the total eggs deposited. If egg-bed mortality is a significant factor due to smothering of eggs in high density masses, or due to heavy predation by larger predators, then these effects would be more likely to have occurred in the late 1960's when stocks of herring and principal groundfish predators were larger (Clark and Brown 1977). Therefore, for the present time series of data, a conservative egg mortality correction factor of 10% might be considered appropriate but was not applied here.

The larval estimate of eggs produced is nearly identical to the VPA egg estimate for the years 1971, 1972, and 1975 with the greatest differences between the two estimates occurring in 1973, 1974 and 1976. VPA fecundity estimates are not available for 1977 and 1978 (Table 4). The VPA/larval ratios are positive in 4 of the 6 years; the 1973 and 1974 ratios are <1. One would expect to get positive VPA/larval ratios assuming significant egg mortality and no other errors in back-calculations of egg production. The 2 years (1973 and 1974) of greatest larval abundance (assumed egg production) in the time series have VPA/larval egg ratios significantly less than 1 as the VPA estimates of eggs produced in 1973 and 1974 are below the lower 95% confidence limit estimates for the larval data (Table 3). An explanation for the lower VPA egg estimates relative to the larval estimates for the 1973 and 1974 year-classes may be due to the higher level of recruitment to the coastal area instead of just to the Georges Bank fishery as observed in recent years by Anthony and Waring (1978). The VPA egg estimate in 1976 are considerably higher than the larval egg estimate by a factor of 6-8, a discrepancy which is difficult to explain since the severe fishing restrictions imposed upon the Georges Bank fishery in 1976, and closed thereafter, did not permit adequate sampling of the major spawning stock of age 3 fish (1973 year-class) upon which VPA estimate of eggs produced is based, so that a ratio <1 would be expected for the 1976 egg ratios. If undersampling of larvae in the Nantucket Shoals area is an important source of error, then this bias would be most pronounced for the 1972, 1973, and 1975-1978 seasons when major spawning occurred in this area. However, no clear pattern for this bias is evident when comparing the VPA and larval egg estimates.

Comparison of Larval Abundance, Survival, Growth, and Recruitment

The initial abundance of herring larvae, average seasonal larval "survival" (inverse of mortality, Table 3) and "growth" are ranked over the 1971-1978 seasons for comparison with available estimates of recruitment at age 3 for the Georges Bank and western Gulf of Maine areas in Table 6. Average "growth" over the season is based on the survey length-frequency data in Table 5. The mean length of larvae attained by a given calendar date (December, February) may be a more meaningful indication of seasonal population growth than the incremental change in length between surveys which can be confounded by intermixing of larval cohorts and differential mortality. Although survey length-frequency distributions are typically polymodal in the autumn because of the variable spawning times, they tend to converge into a single modal length by winter, most likely because of the nature of the larva's decaying exponential Gompertz growth form (Lough et al. 1980). That is, larvae spawned late in the season appear to "catch up" by winter to the length of the larvae that were spawned earlier in the season. Preliminary attempts to follow length modes between successive surveys for precise growth rates were not entirely satisfactory because of the subjective nature of selecting the homologous modal lengths. These data show an increasingly larger mean length of larvae each February from 1974 through 1978. The mean length of larvae in February of 1976, 1977, and 1978 (30-33 mm) were significantly greater (3-5 mm) than that in February 1975 (27.7 mm), and the mean length of larval in February 1975 was nearly 5 mm greater than the mean length of larvae in February 1974 (23.3 mm). Remember from Figure 3 that avoidance of the bongo-nets was believed to be a serious problem for larvae >30 mm. The greater mean length of larvae in February 1976 (1975 year-class) over that in February 1975 (1974 year-class) apparently was maintained through the following late-winter and spring of 1976 based on larval herring survey length-frequency data in 1975 and 1976 reported by Joakimmson (1976), Davis (1975), Davis and Morris (1976), and Grimm (1977).

Estimates of recruitment at age 3 were made from the most recent VPA stock assessment for the Georges Bank and western Gulf of Maine fishery by Anthony and Waring (1980). Recruitment data are available only for the 1968-1973 year-classes for the Georges Bank fishery and they were considered poor for all year-classes since the last strong year-class of 1970 with essentially no fishing in this area after 1976. The western Gulf of Maine estimates of recruitment at age 3 are provided for comparison in Table 6 for the 1971-1977 year-classes since larvae in the Georges Bank - Nantucket Shoals area may be recruiting to the inshore areas. It has been reported by Anthony and Waring (1978) that fluctuations in abundance between the various herring stocks in the Gulf of Maine generally correspond from year to year, implying a common, widespread recruitment mechanism. The 1976 and 1977 western Gulf of Maine recruitment estimates, although preliminary, are considered "good", equal in size to the 1966 year-class which has been used in past assessments as the conventional level of "good" recruitment. All other year-classes 1971-1975, western Gulf of Maine, are considered to have a "poor" level of recruitment.

The 2 years of "good" recruitment assessed for the western Gulf of Maine area, 1976 and 1977, occurred when larval production on Georges Bank-Nantucket Shoals was at or near the lowest level recorded in the 8-year time series. In 1976, the extremely small amount of larvae observed were produced mostly on Nantucket Shoals and in 1977, virtually all the larvae originated on Nantucket Shoals. So far, there is no evidence of recruitment on Georges; instead it appears that only the inshore areas are seeing this recruitment. It is interesting to note that in the Maine juvenile fishery, the 1976 year-class at age 1 (1,300 tons) and the 1975 year-class at age 2 (18,500 tons) were the highest recorded since the 1970 year-class at age 1 and the 1966 year-class at age 2 (Anthony and Waring 1978). Waring and Howe (1979) reported large numbers of juvenile herring occurring in the estuaries of southern Massachusetts by the State Fisheries Surveys, Summer 1978, for the first time in a decade. The post-larvae found in Buzzards Bay in 1978 were believed to belong to the 1977 year-class.

Since the relative rankings of larval abundance, survival, and growth are subjective to a degree, the relationship among these 3 parameters was tested by computing non-parametric Rank-Difference Coefficients, r_d (Tate and

Clelland 1957). The results indicate a positive relationship between larval growth and survival (r_d = 0.67, 10% level of significance), a slight inverse relationship between larval production and growth (r_d = -0.29, N.S.), and essentially no relationship between larval production and survival (r_d = -0.02, N.S). The greatest discrepancy in the rankings between larval survival and growth occurred for the 1973 and 1977 seasons, the highest, and one of the lowest seasons, respectively, of larval production observed in the time series.

Although the time series of data is too short and inadequate to permit firm inferences, it appears that "good" recruitment may be directly related to "good larval growth and survival", which to some extent may be inversely related to the initial abundance of larvae. The 2 years of highest larval production, 1973 and 1974, only had intermediate levels of "growth and survival". The highest "growth and survival" estimates over the time series occurred during the 1975-1977 seasons at the same time there was a shift in the spawning from northeastern Georges Bank to western Georges and Nantucket Shoals.

DISCUSSION

The estimation of larval mortality rates and causes for their differences remain the principal concern of fishery biologists in resolving the fish stock and recruitment problem despite the inherent sampling problems and long-term commitment required for these studies (Hunter 1976). Traditionally, recruitment has been viewed in terms of the critical period concept, i.e., there is a brief period of relatively high mortality during larval life and variation in survival through this period determines the size of the year-class for the most part. One such critical period of high mortality, originally proposed by Hjort (1914), occurs at the end of yolksac resorption when the first-feeding larvae are particularly vulnerable to starvation. Gulland (1965) reevaluated a number of available studies at that time and proposed a set of hypothetical mortality curves of eggs and larvae where differential mortality occurs in an early density-dependent phase over a period of about a month, and subsequently a critical phase, over a relatively short or long period, where high or low mortality can be envisioned leading to variable year-class size. Mortality in the early density-dependent phase may be higher than at any other stage, but not necessarily critical in the sense of determining good and bad year-classes unless it is massive. Subsequent larval studies have not completely validated the critical period concept for all the reasons discussed in recent reviews by May (1974) and Dahlberg (1979).

The generalized shape of larval herring mortality over the first 6 months of life from hatching to near metamorphosis can be depicted as an exponentially declining curve with a loss in numbers of 3-5 orders of magnitude (see Cushing 1974), although considerable variation in these rates for shorter periods has been reported in literature. The autumn-winter average instantaneous mortality rate of 3.3%/day (range 2-5%/day) found for the Georges Bank-Nantucket Shoals larvae in this study is similar to the rates found by Graham and Davis (1971) for western Gulf of Maine larvae and by Wood and Burd (1976) for herring larvae in the central North Sea. High post-yolksac mortality of herring larvae has been observed in laboratory rearing studies by Blaxter (1962) and Laurence (1978 experiment, unpublished data). Laurence's larvae reared at 10^{o}C from eggs collected in the Jeffreys Ledge, western Gulf of Maine area, and fed natural plankton at high densities, had an average daily mortality rate of 12%/day over 13 days with a noticeable increase in mortality 6 days from the midpoint of yolksac resorption, corresponding to the "point-of-no-return" of first-feeding larvae reported by Blaxter and Ehrlich (1974). Field studies appear to substantiate this initial higher than average larval mortality. Saville (1965) reported a marked reduction of spring spawning Scottish Clyde herring larvae shortly after the main hatching peak with apparent mortality rates of 35%/day and 18%/day for the 2 years studied. Dragesund and Nakken (1971) in a 1967 study, estimated 94% mortality over 9 days by the end of yolksac resorption (10-12 mm, mean hatching length _ca_. 9 mm) for Norwegian spring spawning herring larvae, corresponding to an instantaneous mortality rate of 27%/day. And, in a 1969 study (Dragesund and Nakken, 1973) they estimated 70-95% mortality over 14 days (8-19%/day) for early larvae (9-13 mm). Similarly, on this side of the Atlantic, Graham and Chenoweth (1973) estimated 75% mortality over a 4-day sampling period (29%/day) in October 1970 for recently-hatched larvae (<10 mm) spawning on Georges Bank. From these studies, the natural mortality of herring in the first week or two after hatching ranges from 8-35%/day, higher than the average rate of 3-4%/day, as well as the maximum rate (6-8%/day) within a season predicted by the mortality model used in this study corresponding to the inflection point of larval growth. This is not unexpected since the ICNAF surveys were not designed to measure such short-period variations.

Winter mortality estimates of larger herring larvae, corresponding to

Gulland's critical phase, have been made by Graham and Davis (1971) and Graham et al. (1972) for larvae collected in the Sheepscot estuary of Maine during the December-January period. Mortality rates over the 6 years studied, 1964-1969, varied from 22% to 52% per 15 days or, calculated as instantaneous rates from 1.5-3.5%/day. These mortality rates appeared to be reliable to them and more importantly, low mortality was related to good condition of larvae in the winter and subsequently to high abundance of larvae in the spring, which in turn was related to greater percentages of 2-year old fish in the fishery during the 1960's. However, Graham (1980) notes that the correlation between larval abundance and mortality indices and subsequent recruitment to the juvenile herring fisheries apparently brokedown in the 1970's. He believes the poor relationship may be due to an influx of late-spawned larvae into the western Maine estuaries from other spawning areas, apparently as a result of unusual disperal patterns in recent years. A similar range of winter instantaneous mortality rates (<1-5%/day) was estimated by Lough et al. (1979) over 5 December-February periods for Georges Bank-Nantucket Shoals larvae. The 1973-74 and 1974-75 winter periods had relatively high mortality rates of 4-5%/day, whereas the 1975-76, 1976-77, and 1977-78 winter periods had low mortality rates of 1%/day or less. Thus, the available evidence for larval herring in the Gulf of Maine appears to support Gulland's hypothetical mortality curves of an early high density-dependent mortality in the autumn followed by a "critical" density-independent phase of low but differential mortality during the winter. However, the estimation of short-term mortality rates or "critical periods" probably cannot be resolved from the larval herring mesoscale surveys which are on the order of weeks and 10's of kilometers in scale, but they do appear to provide reasonable levels of average seasonal rates. The implication here is that there are at least 3 important periods or stages in the larval life of herring, from hatch to just prior to metamorphosis, that should be studied more intensively: (1) recently-hatched larvae less than 10 mm in length, (2) larger larvae of about 10-20 mm during the autumn, and (3) larvae greater than 20 mm during the overwinter period. Survival, as well as the causes of mortality, appear to be different during each of these periods which are easily masked by the average seasonal picture.

Cushing (1972) has proposed 3 mechanisms governing recruitment in marine fishes: (1) density-independent or environmental factors, (2) density-dependent factors, and (3) competition; all are linked to a single process involving the match or mismatch of larvae and their food organisms. Recent theoretical models by Jones (1973), Jones and Hall (1972), Cushing (1973, 1974, 1975), Cushing and Harris (1973), Ware (1975), Beyer and Laurence (1980) and Beyer (1980) emphasize the link between larval growth and mortality as density-dependent processes regulated by the availability of food. It follows that the degree to which larvae are able to grow rapidly through a succession of decreasing predatory fields, thereby reducing mortality, determines their potential population size. The major causes of larval mortality are believed to be starvation and predation, which may interact. Various mechanisms of density-dependent mortality relating to starvation and predation of fish larvae have been set forth in a recent colloquium by Hunter (1976). The following discussion will highlight aspects of the ICNAF larval herring time series presently under investigation to test various hypotheses about factors controlling recruitment of sea herring in the Gulf of Maine region.

Analysis of the ICNAF larval herring data indicated an inverse relationship between growth and mortality, especially for the years 1975-1977, but this relationship was not readily apparent most years perhaps, because of the difficulties in obtaining precise estimates due to the intermixing of larval cohorts from various spawning areas. A precise estimate of larval herring growth from field collections, based on a relatively new technique of accurately aging larvae from daily growth increments in their otoliths, was made for the 1976 season (Lough et al. 1980). Similar otolith growth data is not available for other seasons in the series. The larger mean size of larvae in December in recent years, and particularly the increased growth or survival of large larvae during the overwinter period from 1975-76 through 1977-78, appears to be the single most important criterion in heralding a large recruited year-class. For these year-classes, 1975-1977, a relatively low overwinter mortality was estimated (<1%/day), as well as a moderate-to-low average autumn-winter mortality (2-3%/day). Studies on other fish stocks also show that good year-classes coincide with years in which large larvae were caught: herring in the North Sea (Saville 1978), North Sea plaice (Simpson 1959, Bannister et al. 1974, Harding et al. 1978), haddock in the North Sea (Saville 1959) and at Faroes (Saville 1956), cod in the Lofoten (Wiborg 1957), and Pacific sardine and anchovy (Ahlstrom 1965). It would be interesting to know if these large larvae were derived from larger individuals as newly-hatched larvae, or whether they grew larger and survived better because conditions were more favorable during the larval period. The higher survival value of large larvae produced from large eggs containing greater yolk reserves has been documented for North Sea herring stocks by Blaxter and Hempel (1963). Reproductively maturing adult females feeding during seasons of increased productivity may provide their offspring with a survival advantage by producing more robust eggs and larvae, thereby providing a direct link between the carrying capacity of the environment and future stock size. However, it is unlikely that the ICNAF larval herring data base will be able to resolve these questions for Atlantic sea herring.

The abundance and patchiness of food for the larvae must play an important role in density-dependent mortality. The causes of winter mortality within the Sheepscot estuary of Maine were inferred to be related to lower lethal temperatures, inhibition of feeding by the low temperatures, as well as a reduction of larval food (Chenoweth 1970, Graham and Davis 1971, Sherman and Honey 1971, Graham et al. 1972). The seasonal variation in the food of larval herring in coastal waters of Maine has been described by Sherman and Honey (1971) and Sherman et al. (1976). A study near completion by Cohen et al. (1980) is examining prey selection and condition of herring larvae in the Georges Bank-Nantucket Shoals area during 3 years, 1974-1976. Major foodprey of larval herring generally reflect the dominant species of copepods available in the size range appropriate to the larva's mouth gape. The dominant prey in 1974 were Pseudocalanus sp. adults, Centropages typicus and C. hamatus copepodites; in 1975, Paracalanus parvus, Pseudocalanus sp., unidentified calanoid adults, and copepod eggs; and in 1976, Pseudocalanus sp., Paracalanus parvus, and unidentified calanoid adults. Population dynamics of the copepods Pseudo-Paracalanus spp. undoubtedly play a dominant role in the feeding and survival of herring throughout the Georges Bank-Gulf of Maine region. These results suggest that the lower mortality rate and greater mean size of larvae during the 1975-76 winter, compared to 1974-75, was coincident with a greater percentage of feeding. Incidence of feeding was significantly greater for the small number of larvae produced during the 1976 season which can be attributed almost entirely to those larvae collected during December 1976 and February 1977 surveys. Condition factor indices also suggest that larvae were more robust the winter of 1976-77 compared to the previous 2 winters.

One hypothesis under investigation is that the greater mixing of waters observed on Georges Bank during February 1976, based on temperature, salinity and wind-stress data, may have provided more favorable conditions for reproduction and growth of a number of endemic copepods. Wind mixing of Georges Bank waters also was very strong during the 1976-77 winter (Wright 1979) when larval mortality was low. The 1976 and 1977 year-classes are predicted to have very high recruitment in the inshore areas (Anthony and Waring 1980) so that the wind mixing-increased productivity hypothesis is very attractive in explaining recruitment throughout the Gulf of Maine region. Cohen and Wright (1980) proposed that the reason Georges Bank is so productive is because it is always well-mixed on the shoal central portion. The strong tidal currents and frequent storms characteristic of the region are believed to be the important physical mechanisms by which a high level of nutrients are supplied to the Bank through regeneration of nutrients from the bottom sediments and from the deep nutrient-rich waters on both sides of the Bank. The relation between the timing and vertical and horizontal extent of chlorophyll maximum layers required for survival of Pacific anchovy larvae has been shown by Lasker (1975). The spatial and temporal patchiness of larval herring food organisms, primarily copepods, is dependent upon the phytoplankton distribution and ultimately, the physical forcing mechanisms hypothesized for the Georges Bank area.

Another broadscale hypothesis under study is the relation between temperature and the increased levels of zooplankton productivity in recent years. A general warming trend of 2-3°C during the autumn (reference date 7 November) has been observed by Davis (1978) for Georges Bank bottom-water temperatures, particularly since 1971, peaking in 1973, 1974, 1976, and 1977. Davis reported the highest adjusted mean temperatures on Georges Bank in a decade during the autumn of 1976 and 1977, the 2 years for which high recruitment is predicted for the inshore Gulf of Maine herring fishery. The trend in zooplankton biomass on Georges Bank from autumn 1971 through 1977 reported by Sherman et al. (1978) followed the general warming trend. The plankton biomass data for 1976 are not yet available, but if there is a correlation between water temperature and plankton biomass, and if the zooplankton biomass represents food availability for the larvae, then the 1976 and 1977 autumns of high temperature and high biomass would point to important relationships linking the environment with larval feeding, growth, survival and recruitment.

There is no direct evidence on the mechanisms by which temperature operates other than when it reaches the lower limit for survival which is probably unlikely for larvae in the Georges Bank area since they are not exposed to the extremes of their temperature limits (Blaxter 1960) compared to the nearshore area. Benko and Siliverstov (1971) found significant positive correlations between year-class strength and surface-water temperature over the spawning grounds and in the area along the larval drift for Norwegian spring-spawning herring. They attributed 22-59% of the variability in year-class strength to temperature effects during the period, inferring that warm temperatures, signaling the onset of spring plankton populations, were related to more favorable feeding conditions for the larvae. Postuma (1971) also found a significant relationship between year-class strength and temperature conditions on the spawning grounds of autumn-spawning North Sea herring which he believed may operate through differential egg mortality at different temperatures. He also indicated from the field data and from the laboratory work of Blaxter (1956) that hatching success, and consequently year-class strength, was related to spawning temperature by a dome-shaped curve with optimum conditions around 12°C. In addition, he noted that higher temperatures in the coastal nursery areas for 6 month-old larvae in the following spring were related to recruitment strength, which again indicated good feeding conditions.

The role of temperature as it may affect the location and timing of spawning and hatching success in the Georges Bank-Nantucket Shoals area is questionable. Peak early maturation time of herring on Georges Bank has been correlated with bottom temperature in August by Berenbeim and Sigaev (1978). However, it was noted that on Georges Bank the onset of spawning has been delayed and the length of the spawning season has shortened significantly after the 1975 season which followed the warming trend in average bottom-water temperatures reported by Davis (1978). Another factor, however, which probably contributed more to the delayed spawning in recent years is the shift of major spawning activity from eastern Georges to western Georges and Nantucket Shoals where spawning normally is later. And also, there is the possibility that the shift in the spawning season between the late 1960's and early 1970's, prior to the strong 1970 year-class spawning for the first time in 1973, may have been associated with the average age composition of the stock. Larger, older fish in a population are believed to spawn before the younger fish (Boyar 1968), and with the rapid decline of the stocks in the late 1960's, the average age of the populations was much younger in the 1970's. The optimum temperature for herring spawning in the Gulf of Maine region is stated in the literature as 9.5°C which coincides with the bottom temperature observed (9.5-10°C) over 6 years on Jeffreys Ledge (McCarthy et al. 1979). However, bottom temperatures over spawning beds on northeast Georges Bank, estimated from the distribution of <8-mm larvae (S. Grimm, unpublished data), are generally higher than this. Some of these egg beds along the northern edge of Georges would experience wide temperature fluctuations (from 6-13^{o}C) with the north-south excursion of strong temperature fronts over a single tidal cycle (Trites 1978). This contrasts with only 1-2^{o}C change over a tidal cycle in the Jeffreys Ledge area. It is possible that the timing of spawning on northeast Georges may be more closely related to the position of the front relative to the historical beds, and the minimum or maximum temperatures associated with the front, than to the mean temperature. In any case, the sampling of temperature in space and time on the standard ICNAF grid is so sparse in relation to the large short-term fluctuations associated with the front, that mean temperature data would not be expected to be closely correlated with spawning time.

The importance of larval dispersal to recruitment of fish stocks, especially where spawning stocks occupy relatively isolated banks surrounded by deep oceanic water has been emphasized by Fraser (1958) and Saville (1965). Small changes in current patterns can cause extreme fluctuation in the retention and survival of larvae on such exposed banks. How so many populations of fish maintain themselves on Georges Bank in the face of what appears to be frequent offshore transport of surface waters was the subject of a paper by Colton and Temple (1961). Two studies have made preliminary summaries of dispersal of larval herring on Georges Bank using the ICNAF survey data. Bumpus (1976) looked at 3 length groups by 5-mm intervals of larvae from recently-hatched up to 20 mm, comparing their spread between successive cruises from the 1972-1974 seasons with monthly Ekman transport indices, and showed that the drift of larvae was generally southwest over Georges Bank which is consistent with mean advection. Lough et al. (1979) examined changes in the distribtuion of all length groups of larvae between cruises over the autumn and winter in relation to weekly Ekman transport indices for the 1971-1977 seasons because significant short-term variations have been masked by monthly averages and in this area important wind-driven events occur at about 100 hour (4-5 day) intervals (Ramp and Vermersch 1978, Beardsley et al. 1978). In this study only a general correspondence was found in the direction and magnitude of larval dispersal, but more so during periods of unusually high Ekman transport. The lack of a clear relationship between Ekman transport and larval dispersal is not surprising since the average interval (3 weeks) between ICNAF surveys was too long to observe effects of major wind events. Bumpus (1976) states that in the shallow waters of Georges Bank and Nantucket Shoals, water movement may be more directed downwind. Nevertheless, it was noted that over the entire ICNAF series (except for December 1975) herring larvae were largely restricted inside the 100-m depth contour on Georges Bank and Nantucket Shoals. In December 1975 there appeared to have been transport of larvae into the Gulf of Maine, but by February 1976 the larvae were back in their usual distribution pattern.

The development of anticyclonic warm-water eddies north of the Gulf Stream moving near the southern edge of the Georges are believed to play an important role in the movement of shelf/slope waters both on and off the Bank. Anticyclonic eddies occurred near the southern edge of Georges Bank in autumn 1972, 1974, 1975, February-April 1976, and throughout the year in 1977 and 1978 (Bisagni 1976, Chamberlin 1978, Mizenko and Chamberlin 1979, Celone and Chamberlin 1980). Although there is no firm evidence of entrainment of larvae by these passing eddies, transport of herring larvae across the 100-m depth contour occurred frequently through ICNAF time series, both south across the shelf/slope water front and north into the Gulf of Maine, but the loss appeared to be small relative to the total population. Some portion of the larval population always remained within the central part of the bank through the winter and spring. Preliminary studies of the vertical distribution of herring larvae in the Georges Bank-Nantucket Shoals and western Gulf of Maine region made by Lough (1975) and Potter and Lough (1980) show early larvae broadly spread throughout the water column, centered around the mean depth to bottom, and larger-older larvae concentrated near the bottom or surface at times. The short-term effects of winds, even if severe, may affect only the upper few meters of water column so that wind transport may be small relative to transport by the long-term residual or Shelf Water/Slope Water interaction. Warm-core eddies moving south of Georges entrain a significantly greater volume of water off the banks affecting larvae deeper in the water column. Advective processes may play a more important role when larvae are small but as they grow larger, their increased ability to perform vertical migrations (see Siliverstov 1974 for review) may aid them in maintaining their position on the banks. Vertical migration coupled with the strong, semi-diurnal, rotary, tidal currents that are a distinctive feature of Georges Bank may be an important retention mechanism for larval herring and other endemic zooplankton.

Analyses are in progress on the vertical (using electronically-controlled opening-closing sampler - MOCNESS[1]) and horizontal movements of chaetognaths on Georges Bank in relation to direct measures of tidal and residual currents, and on a small patch of herring larvae in the Nantucket Shoals are sampled intensively during the 1978 patch study (Lough 1979). Results from these studies may lend support to the retention hypothesis.

There is little evidence for naturally occurring intraspecific and interspecific competition of fish larvae for available food. Wyatt (1974) has provided some evidence for a possible competitive situation between plaice and sand eel larvae feeding on _Oikopleura dioica_. The Pacific sardine-anchovy relationship has been under investigation for many years (Ahlstrom 1965, 1967), but it was inferred that mortality caused by competition for food between the co-occurring larvae did not seem to be as important as predation of adults. Laurence et al. (1980) found that cod larvae grew larger and survived better than haddock larvae when reared together at densities higher than normally occurs in nature, implying direct competition between the 2 species; however, the experimental results may be interpreted as a result of predation by cod larvae on haddock and cannabilism by cod, which may have stemed from the initial size range of prey organisms suppled. Total ichthyoplankton from the ICNAF time series are presently being analyzed, however, findings for 3 years in the series, the 1974-1976 seasons, have been reported by Bolz et al. (1980) for the separate areas of Georges Bank and Nantucket Shoals within the 100-m contour. Hake larvae were dominant in early autumn, herring larvae from mid-autumn to early winter, and cod, pollock, haddock, and sand lance from winter through spring. The 3 or 4 dominant species on each survey composed greater than 80% of the total abundance of larvae collected from either area. Although the dominant species remained much the same for the 3 years, important differences in their relative rankings and geographic distribution were noted. Sand lance larvae were overwhelmingly dominant on both Georges Bank and Nantucket Shoals during the February and April cruises in 1976. Their dramatic increase in abundance during the 1974-1977 winters between Cape Hatteras and Georges Bank was documented by Smith et al. (1978). During the 1976 season, the abundance of all larvae decreased dramatically in both areas compared to previous years. Sand lance larvae only remained dominant in February 1977 on Nantucket Shoals. Very low densities of ichthyoplankton were observed particularly on Georges Bank, during autumn and winter 1976-77 when extremely strong and persistent southerly transport of waters was inferred (Ingham 1979). Peaks of larval abundance generally are successive and their larval population centers tend to be geographically separated. When dominant larval species co-occur in time and area, such as herring and sand lance, their length modes usually differ significantly, thereby partitioning the size spectra of available food organisms. Our preliminary gut analyses of both species support this view. It appears, therefore, that direct competition between larval fish for the same food organism is limited.

The role of predation on larval fish populations, other than on demersal egg beds mentioned previously in this paper, is difficult to ascertain as there is very little quantitative information available, and there is the problem of separating starvation from predation mortality. The only study providing quantitative, concurrent field estimates of starvation vs. predation larval fish mortality is that of O'Connell (1980) on northern anchovy larvae in the Southern California Bight, March 1977. He observed that starving larvae, based on histological methods, accounted for about 8% of the population, for an estimated average daily mortality rate of 21%, or 40% of the average total daily mortality for the 7.5-mm SL group. O'Connell's study represents a new approach to estimating the magnitude of larval mortality and it needs to be applied to population studies for a number of years to see if it correlates well with a recruitment index. Many species of fish and zooplankton are known to prey upon fish larvae (Lebour 1922, 1923; Pearcy 1962, Fraser 1969, Lillelund and Lasker 1974, Daan 1976, von Westerhagen and Rosenthal 1976, Harding et al. 1978). Medusae, chaetognaths, and larger fish have been considered as major predators of larval fish. Ctenophores, euphausiids, and amphipods also can be important predators in the Georges Bank area. Dense concentrations of the siphonophore, Nanomia cara, normally found in the Gulf of Maine waters, were observed throughout Georges Bank during the autumn-winter of 1975-76 (Rogers et al. 1978). Recall the unusual transport of herring larvae into the Gulf of Maine during December 1975. Dense concentrations of the chaetognath, Sagitta elegans, also are found on Georges Bank and Nantucket Shoals (Redfield and Beale 1940, Clarke et al. 1943, Lough 1979) and could possibly account for heavy predation of small fish larvae (Kuhlmann 1977). However, chaetognaths, as well as other zooplankton, may play a more important role as potential competitors for the same food organisms or, at high densities they may disrupt normal feeding behavior of larvae or reduce the impact of predation mortality by larger predators. An assessment of the co-occurrence of some of the smaller potential predators of larval herring in the Georges Bank area will have to wait until zooplankton data from the same ICNAF time series are fully processed and summarized.

While starvation and predation may be the major causes of larval mortality, they need to be viewed in the context of population dispersal as affected by changing current patterns. Detailed knowledge of the hydrography and biology of the region is needed to assess the availability of larval food organisms and the impact of potential predators. In the case of the Georges Bank-Nantucket Shoals herring, we have seen that in most years there appear to be sufficient numbers of larvae produced to result in a strong recruited year-class if conditions are favorable.

Recruitment success appears to be determined by a matrix of complex factors operating during the larval period over the wide range of stock sizes examined. However, to begin to understand the mechanism through which environmental variation affects larval survival, it will be necessary to construct and test specific hypotheses through intensive, interdisciplinary studies of small and mesoscale interactions such as the Georges Bank 1979 Larval Herring Patch Study (Lough 1979) and the 1978 Plaice Egg Patch Study in the Southern Bight of the North Sea (Ramster 1978, Hill and Harding 1978).

SUMMARY

1. Larval herring catches from 39 ICNAF surveys covering the Georges Bank - Nantucket Shoals area over 8 spawning seasons, autumn-winter 1971-1978, were used to estimate their abundance, mortality, and growth during the first 6 months of life for comparison with available spawning stock, recruitment and environmental data.

2. Spawning of the demersal eggs occurs in shoal waters on historic egg-bed sites in the northern part of Georges Bank and Nantucket Shoals from September through December, peaking in October-early November each year, but predominately in one area or the other over the time series. In recent years, the onset of spawning was delayed and the length of the spawning season shortened, particularly after 1975, coinciding with what was apparently the collaspe of the

fishery on northeastern Georges Bank in 1976 and a shift in the remaining spawning population to northwestern Georges Bank and Nantucket Shoals.

3. Seasonal larval abundance estimates were made using night-day adjusted catches by the expanded day and area method where for each survey, the mean density of larvae was estimated for each millimeter length class by the delta-distribution within the 7-30-mm fully vulnerable size classes and multiplied by the number of days represented by the survey and by the Georges Bank-Nantucket Shoals study area. Length-specific mortality rates were estimated for each season by the exponential regression of larval abundance on the 7-30-mm length classes. An estimate of the initial abundance of larvae with confidence limits for each season was made by extrapolating the exponential regressions back to 5.66 mm, the mean size at hatching. Mortality as a function of age was estimated by coupling the length-specific exponential regression equations with a Gompertz growth curve describing larval herring growth in length over time from hatch to near metamorphosis.

4. The initial abundance of larvae at hatching produced in the Georges Bank - Nantucket Shoals area was estimated to be relatively high in 1973 and 1974 (79-121 x 10^{12} larvae), intermediate in 1971, 1972, and 1975 (20-43 x 10^{12}), low in 1977 and 1978 (2-5 x 10^{12}), and extremely low in 1976 (<1 x 10^{12}). Upper and lower 95% confidence limits lie within the range of approximately half to double the initial abundance estimates.

5. Age-specific instantaneous mortality rates over the autumn-winter period were low for the 1975 and 1976 seasons (2.2-2.7% per day), intermediate for the 1973, 1974, and 1977 seasons (3.0-3.4% per day), high for the 1971 and 1972 seasons (3.9% per day), and highest of all for the 1978 season (4.6% per day). The combined, overall average mortality rate for the autumn was 4.4% per day; the winter, 1.1% per day; and for the autumn-winter period, 3.3% per day.

6. A comparison was made of the potential egg production derived from the most recent VPA assessment of the Georges Bank adult spawning stock which provided a scaled and a constant fecundity estimate for the years 1971-1976, and derived from the initial larval abundance estimates, assuming no egg-bed mortality between the time of spawning and hatching. VPA/larval egg ratios were near

unity for the years 1971, 1972, and 1975. The 2 years (1973 and 1974) of greatest larval abundance in the time series had egg ratios significantly less than 1 (0.2-0.6 range), and 1976, the year of lowest larval abundance, had positive egg ratios of 6-8. Reasons for these discrepancies are not readily explained.

7. Growth of larvae based on survey mean length was increasingly greater each succeeding February from 1974 through 1978 (1973-1977 year-classes). Estimates of larval abundance, survival, and growth were compared with available data on recruitment at age 3 over the time series. Corresponding recruitment data from the Georges Bank fishery only was available for comparison with the 1971-1973 year-classes and it was considered poor for all 3 of these years and collapsed in this area after 1975. However, since there is evidence of recruitment to the inshore areas in recent years, and the fact that year-class size tends to correspond throughout the Gulf of Maine region, the western Gulf of Maine recruitment indices were used to extend the time series comparison through 1977. There is evidence to suggest that the 1976 and 1977 year-classes showing good recruitment in the inshore areas can be directly related to good larval survival and growth, which is inversely related to their initial abundance to a lesser degree. The highest larval growth and survival estimates occurred during the 1975-1977 seasons of relatively low production when the shift in the spawning occurred from Georges Bank to the inshore Nantucket Shoals. The single most important criterion for predicting the entry of a large recruited year-class is the occurrence of these large larvae (>30 mm) surviving through the winter.

8. It appears that in most years, over the time series studied, sufficient numbers of larvae are produced and retained on the Georges Bank and Nantucket Shoals spawning areas to result in a strong recruited year-class if conditions are favorable. The winter period appears to be critical in the sense that variations in larval growth and survival can be observed from year to year that can be related to good or poor recruitment, however, conditions during the autumn also appear to have important effects on growth and survival of larvae. Favorable conditions for good survival of herring larvae appear to be related to an increase in the abundance of their principal food prey, the copepods _Pseudo-Paracalanus_ spp. Two broad-scale hypotheses proposed to explain the increased

levels of zooplankton are: 1) the increased wind mixing-nutrient regeneration observed during the winters of 1976 and 1977 and, 2) the higher than average autumn bottom-water temperatures observed in recent years in the Georges Bank area, but the linking mechanisms still need to be clarified. The importance of water mass frontal interaction, both north and south of Georges Bank, on populations of organisms living there, and the full impact of Gulf Stream generated warm-core eddies moving south of Georges is largely unknown.

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TEXT FOOTNOTES

1. Multiple Opening/Closing Net and Environmental Sensing System, after Wiebe et al. (1976).

Table 1. Summary of 39 ICNAF larval herring cruises conducted in the Georges Bank - Nantucket Shoals area, 1971-1978 seasons.

Vessel	Cruise no.	Dates	Area surveyed ($\times 10^{-9} m^2$)	Percentage positive area for larvae	Sample mesh size used	
					0.333 mm	0.505 mm
		1971 season				
CRYOS	71-01	9-24 Sep. 1971	78.88	17.7		✓
DELAWARE II	71-04	21 Sep.-4 Oct.	82.36	26.8		✓
VIANDRA	71-01	9-25 Oct.	77.14	60.2	✓	
W. HERWIG	71-07	28 Oct.-12 Nov.	81.20	47.1	✓	
ALBATROSS IV	71-07	2-17 Dec.	83.52	55.6		✓
		1972 season				
ARGUS	72-01	22-30 Sep. 1972	52.20	17.3		✓
WIECZNO	72-01	2-28 Oct.	92.80	46.3	✓	
ARGUS	72-02	12-28 Oct.	87.00	58.7	✓	
A. DOHRN	72-01	31 Oct.-12 Nov.	90.48	66.7	✓	
ALBATROSS IV	72-09	2-20 Dec.	93.96	61.7		✓
		1973 season				
CRYOS	73-01	16-28 Sep. 1973	51.04	13.6	✓	
WIECZNO	73-40	28 Sep.-20 Oct.	92.80	42.5		✓
BELOGORSK	73-01	15 Oct.-1 Nov.	93.96	70.4	✓	(Stas. 27&84 substitution)
W. HERWIG	73-43	28 Oct.-8 Nov.	92.80	77.5	✓	
ALBATROSS IV	73-09	4-20 Dec.	95.12	86.6	✓	
ALBATROSS IV	74-02	11-22 Feb. 1974	66.12	54.4		✓
		1974 season				
WIECZNO	74-01	27 Sep.-10 Oct. 1974	96.28	24.1		✓
PROGNOZ	74-01	18-30 Oct.	91.64	72.2	✓	
A. DOHRN	74-01	16-23 Nov.	81.20	81.4	✓	
ALBATROSS IV	74-13	4-19 "	96.28	74.7	✓	
ALBATROSS IV	75-02	12-28 Feb. 1975	91.64	48.1	✓	
		1975 season				
BELOGORSK	75-02	29 Sep.-8 Oct. 1975	93.96	15.4		✓
BELOGORSK	75-03	17-30 Oct.	95.12	60.4	✓	
A. DOHRN	75-187	1-18 Nov.	100.92	70.1	✓	
ALBATROSS IV	75-14	5-17 Dec.	96.28	62.7	✓	
ALBATROSS IV	76-01	10-23 Feb. 1976	99.76	45.4	✓	
		1976 season				
BELOGORSK	76-03	4-11 Oct. 1976	47.56	28.1	✓	
WIECZNO	76-03	14 Oct.-3 Nov.	96.28	13.4	✓	
A.DOHRN	76-02	15-29 Nov.	96.28	20.5	✓	
RESEARCHER	76-01	27 Nov.-11 Dec.	84.68	31.9	✓	
MT. MITCHELL	77-01	13-24 Feb. 1977	95.12	23.5	✓	
		1977 season				
WIECZNO	77-06	4-24 Oct. 1977	63.80	21.8		
A. DOHRN	77-03	1-18 Nov.	93.96	49.4	✓	
DELAWARE II	77-13	8-20 Dec.	68.44	34.8		✓
ALBATROSS IV	78-02	14 Feb.-8 Mar. 1978	96.28	16.9	✓	
		1978 season				
WIECZNO	78-04	14 Oct.-1 Nov 1978	71.92	37.1	✓	
A. DOHRN	78-03	26 Oct.-17 Nov.	83.52	9.7	✓	
ALBATROSS IV	78-15	29 Nov.-12 Dec.	93.96	13.6	✓	
MT. MITCHELL	79-02	15-24 Feb. 1979	54.52	0.0		✓

Table 2. Estimated seasonal hatching dates and spawning grounds of Atlantic sea herring for the 1971-1978 seasons, Georges Bank and Nantucket Shoals area. Spawning season and area are based on abundance estimates for the occurrence of recently-hatched larvae less than 10-mm SL.

Season	Hatching Dates Combined Area	Weighted Middate	Length of Season (Days)	Spawning Area[1]	
				Georges Bank	Nantucket Shoals
1971	10 Sep-26 Dec	15 Oct	107	96%	4%
1972	16 Sep-28 Dec	22 Oct	103	14	86
1973	9 Sep-29 Dec	25 Oct	111	56	44
1974	28 Sep-22 Dec	2 Nov	85	86	14
1975	20 Sep-27 Dec	30 Oct	98	34	66
1976	10 Oct- 8 Nov	24 Oct	29	3	97
1977	1 Oct-14 Dec	24 Oct	74	<1	99
1978	16 Oct-19 Dec	8 Nov	64	<1	99

[1] Percentage of small larvae (<10 mm SL) originating in each area.

Table 3. Larval herring estimated length-specific mortality rates, abundance at a hatching length of 5.66 mm, and average age-specific mortality over 3 periods (autumn, winter, autumn-winter) from hatching through 150 days of age for the 1971-1978 seasons, Georges Bank-Nantucket Shoals area.

Season	[1] Z_L	[2] SE (Z_L)	[3] R	[4] Estimated Abundance (A_L x 10^{-12}) Predicted	Lower CL	Upper CL	[5] Average Mortality ($\hat{M}_x$) 0-100	100-150	0-150 Days
1971	0.2449	0.0273	0.886	42.857	18.848	97.446	0.053	0.013	0.040
1972	0.2468	0.0304	0.877	23.385	9.651	56.664	0.053	0.013	0.040
1973	0.1892	0.0231	0.868	120.920	60.312	242.435	0.041	0.010	0.030
1974	0.1965	0.0099	0.973	79.029	58.597	106.585	0.042	0.010	0.032
1975	0.1652	0.0175	0.895	20.905	12.333	35.432	0.036	0.009	0.027
1976	0.1352	0.0205	0.815	0.924	0.498	1.713	0.029	0.007	0.022
1977	0.2101	0.0263	0.862	4.585	2.076	10.128	0.045	0.011	0.034
1978	0.2950	0.0324	0.911	2.896	1.308	6.412	0.063	0.015	0.047

[1] Z_L = The instantaneous rate of decline in abundance with length (7-30-mm length classes).

[2] SE (Z_L) = Standard error of Z_L.

[3] R = Correlation coefficient (length with log abundance).

[4] Estimated Initial Abundance ($\hat{A}_L$) = Predicted abundance at a length of 5.66 mm with lower and upper 95% confidence limits (CL).

[5] Average Mortality ($\hat{M}_x$) = The instantaneous rate of decline in abundance with age (x=days) averaged over 3 periods from hatching.

Table 4. Comparison of potential egg production from the Georges Bank-Nantucket Shoals area, 1971-1978 seasons, determined from VPA stock size (Age 3+) and larval catch estimates.

Year	VPA Adult Stock Estimate of Eggs Produced: (1) Scaled Fecundity ($x10^{-12}$)	(2) Constant Fecundity ($x10^{-12}$)	Larval Estimate at Hatching ($x10^{-12}$)	Ratio: VPA (1)/Larval Estimate	VPA (2)/Larval Estimate
1971	59.4	56.2	42.9	1.4	1.3
1972	30.8	26.9	23.4	1.2	1.2
1973	33.0	27.7	120.9	0.3	0.2
1974	44.5	38.1	79.0	0.6	0.5
1975	25.2	21.7	20.9	1.2	1.0
1976	7.1	5.9	0.9	7.9	6.6
1977	----	----	4.6	---	---
1978	----	----	2.9	---	---

Table 5. Summary of larval herring length and growth survey data for the Georges Bank - Nantucket Shoals area, 1971-78 seasons. Side-scored growth increment represents an average autumn rate, October-December.

Survey middate	Length range (mm)	Mean length (mm)	Standard deviation	Growth increment (mm/day)	
1971 Season					
16 Sep 71	4-14	7.8	1.4	-	
27 Sep	5-25	8.2	2.6	0.03	
17 Oct	6-30	12.5	4.9	.20	
5 Nov	5-31	12.7	4.0	.01	
9 Dec	6-30	18.3	2.9	.16	.11
1972 Season					
26 Sep 72	6-22	9.4	1.8	-	
14 Oct	6-24	11.9	3.3	.13	
20 Oct	5-23	9.6	3.1	-	
5 Nov	3-28	12.9	3.5	.19	
10 Dec	6-30	15.7	3.7	.08	.07
1973 Season					
19 Sep 73	5-11	7.0	0.9	-	
9 Oct	4-22	7.3	3.1	.01	
23 Oct	5-26	11.8	3.7	.30	
2 Nov	6-28	11.8	4.3	0	
13-Dec	5-31	17.0	4.9	.12	.15
14 Feb 74	5-33	23.3	4.3	.10	
1974 Season					
7 Oct 74	3-26	5.7	1.3	-	
24 Oct	5-20	8.3	1.8	.14	
19 Nov	6-23	12.8	3.5	.17	
13 Dec	2-33	16.9	4.8	.16	.17
14 Feb 75	8-40	27.7	3.8	.17	
1975 Season					
1 Oct 75	5-18	6.5	1.3	-	
23 Oct	5-23	7.9	1.7	.06	
9 Nov	2-24	11.8	3.7	.13	
9 Dec	6-29	17.5	3.7	.18	.17
16 Feb 76	12-39	30.5	4.6	.19	
1976 Season					
8 Oct 76	5-16	8.7	1.6	-	
24 Oct	6-21	11.2	3.0	.15	
22 Nov	9-27	19.6	2.9	.28	
4 Dec	7-29	18.9	5.1	-	.18
18 Feb 77	21-36	30.8	3.4	.15	
1977 Season					
14 Oct 77	5-23	8.3	1.3	-	
9 Nov	6-24	14.8	2.3	.22	
14 Dec	13-28	22.9	2.9	.22	.23
24 Feb 78	22-41	32.9	4.7	.14	
1978 Season					
24 Oct 78	2-20	8.0	2.4	-	
6 Nov	3-17	7.5	3.4	-	
5 Dec	5-27	14.0	5.7	.22	.14
19 Feb 79	-	-	-	-	

Table 6. Ranked comparison of the Georges Bank-Nantucket Shoals larval herring initial abundance, average seasonal "survival and growth", and an estimate of recruitment at age 3 for the Georges Bank and western Gulf of Maine spawning areas, 1971-1978 seasons. A rank of 1 represents the highest value. VPA estimates of herring stock size at age 3 for the Georges Bank herring fishery are only available for the 1968-1973 year classes.

Year	Spawning[1] Area	Larval			Recruitment at Age 3 ($x10^{-6}$)	
		Abundance	"Survival"	"Growth"	Georges Bank	W. Gulf of Maine[2]
1971	GB (96%)	3	6	5	112.7	98.1
1972	NS (86%)	4	7	7	34.4	53.3
1973	GB (56%)	1	3	6	67.1	146.2
1974	GB (86%)	2	4	4	----	60.3
1975	NS (66%)	5	2	3	----	101.7
1976	NS (97%)	8	1	2	----	(269+)
1977	NS (99%)	6	5	1	----	(269+)
1978	NS (99%)	7	8	8	----	----

[1] GB = Georges Bank
NS = Nantucket Shoals
Percentage of small larvae (<10 mm) originating in area within parentheses.

[2] Western Gulf of Maine 1976 and 1977 recruitment estimates within parentheses are preliminary.

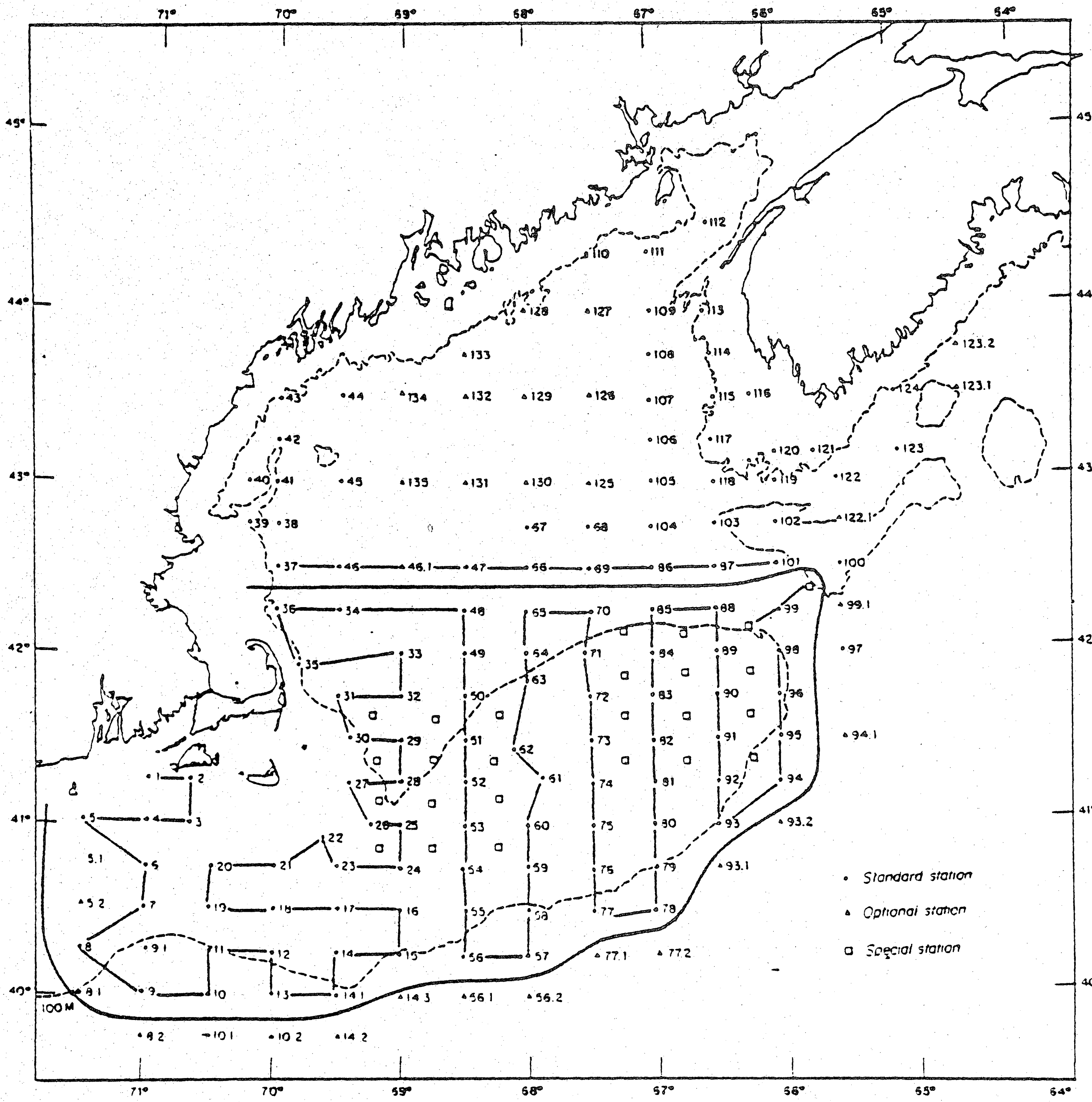

Fig. 1. Station plot for ICNAF Larval herring surveys with a standard cruise track drawn for the Georges Bank-Nantucket Shoals area. Station sampling within the encircled dark line has been emphasized since 1974, and this area represents our best coverage for the entire larval herring time series. Stations 1-36 represent the Nantucket Shoals area, and Stations 48-99 represent the Georges Bank area. Standard station (closed circles) outside the encircled area are sampled as time permits. Open squares are examples of special stations where additional sampling may be made in areas of high larval densities. Triangles represent optional stations as time permits.

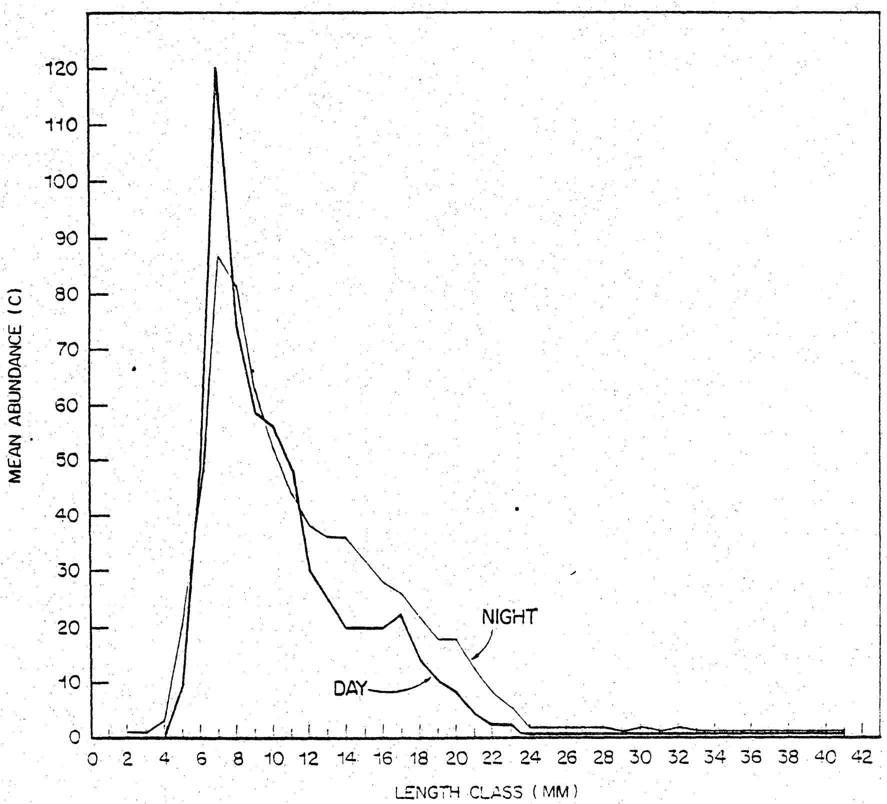

Figure 2. Comparison of night and day larval herring catches by 1-mm length class. Mean abundance (c) values are based on data from 35 surveys, 1971-1977 seasons, Georges Bank - Nantucket Shoals area.

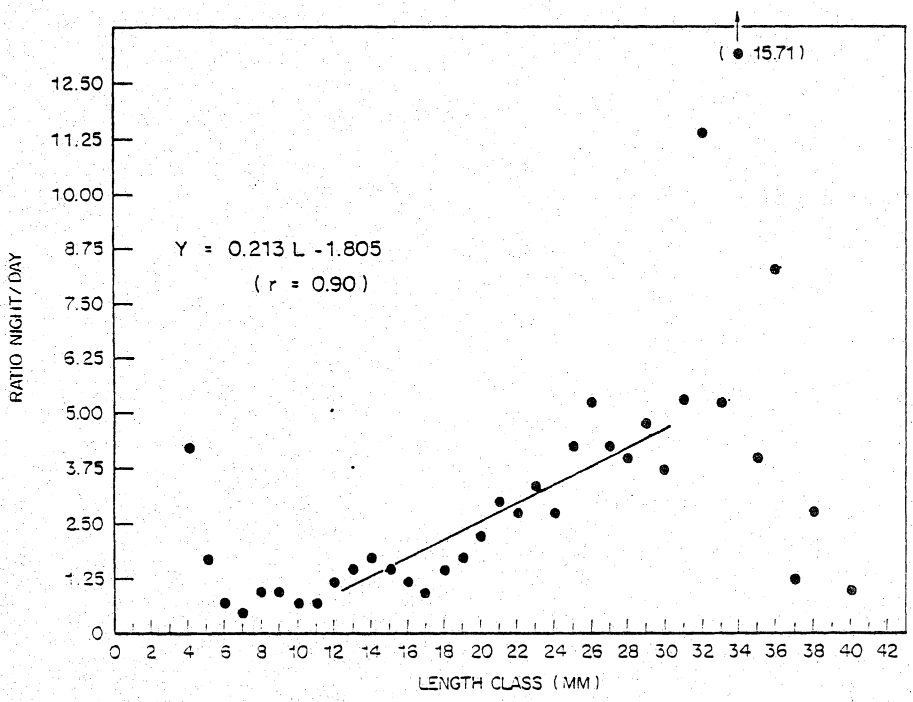

Figure 3. Night to day ratios of larval mean abundance (c) by 1-mm length classes from the same data shown in Figure 2. A regression line (equation insert) is fit to the ratios for the 13-30-mm length classes.

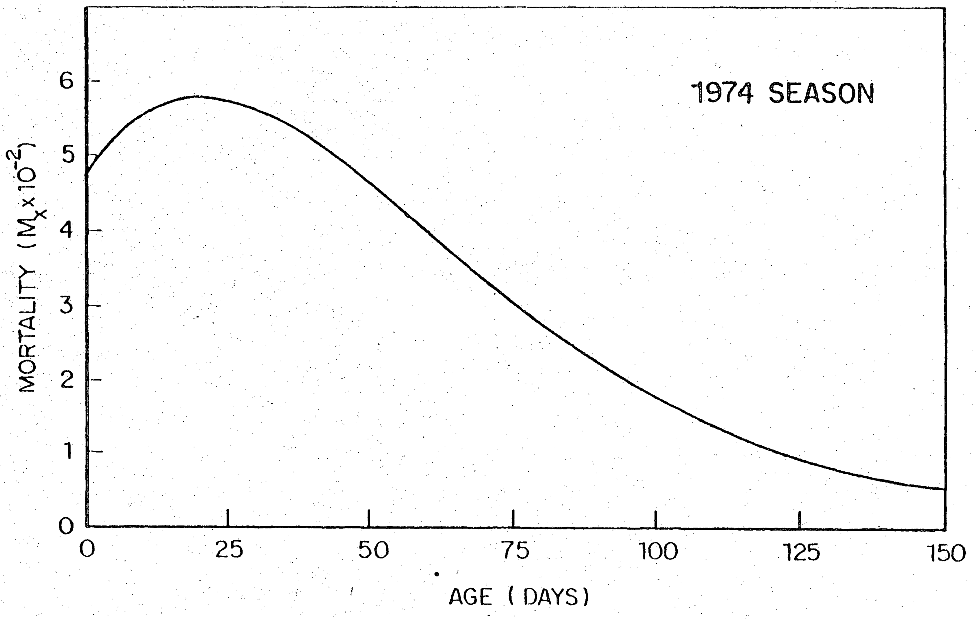

Figure 4. Example plot (1974 season) of the change in the instantaneous mortality rate, M_x, with respect to age of larval herring as a reflection of the functional form of the Gompertz growth model which has an inflection point at 20.28 days from hatching.

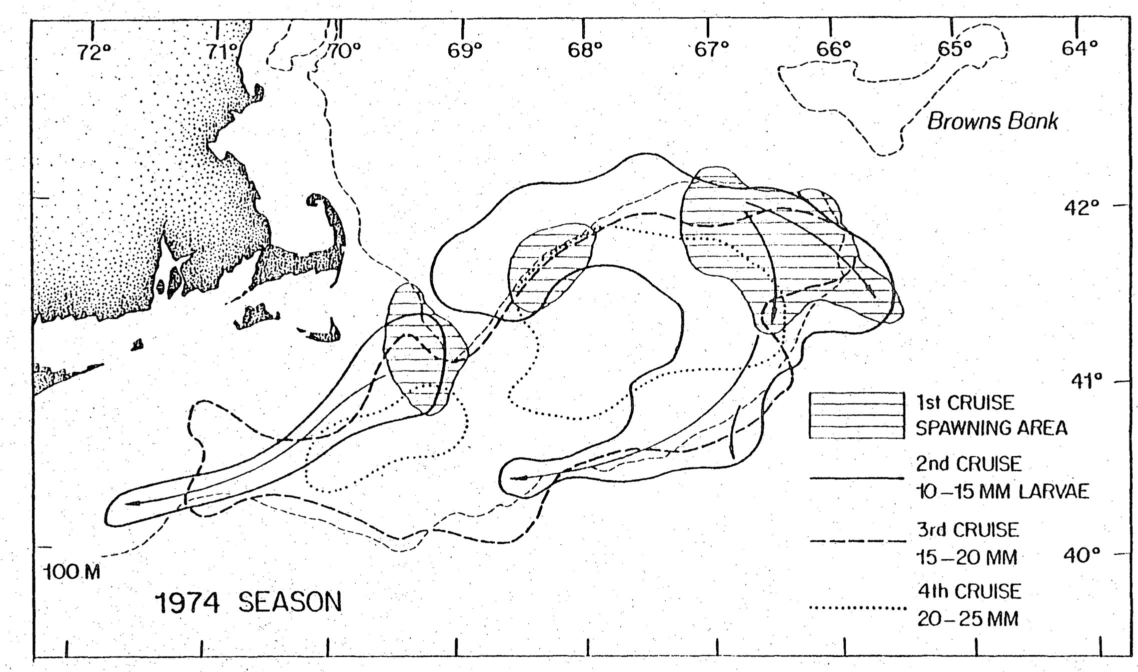

Figure 5. Example of the spread and inferred dispersal (arrows) of a cohort of herring larvae from spawning areas on Georges Bank and Nantucket Shoals over 4 cruises conducted during the 1974 season from October through December. Main larval concentrations enclosed for each survey were identified by having station densities greater than 10 larvae per 10 m^2, except for the 4th cruise where concentrations were identified by having greater than 5 larvae per 10 m^2.

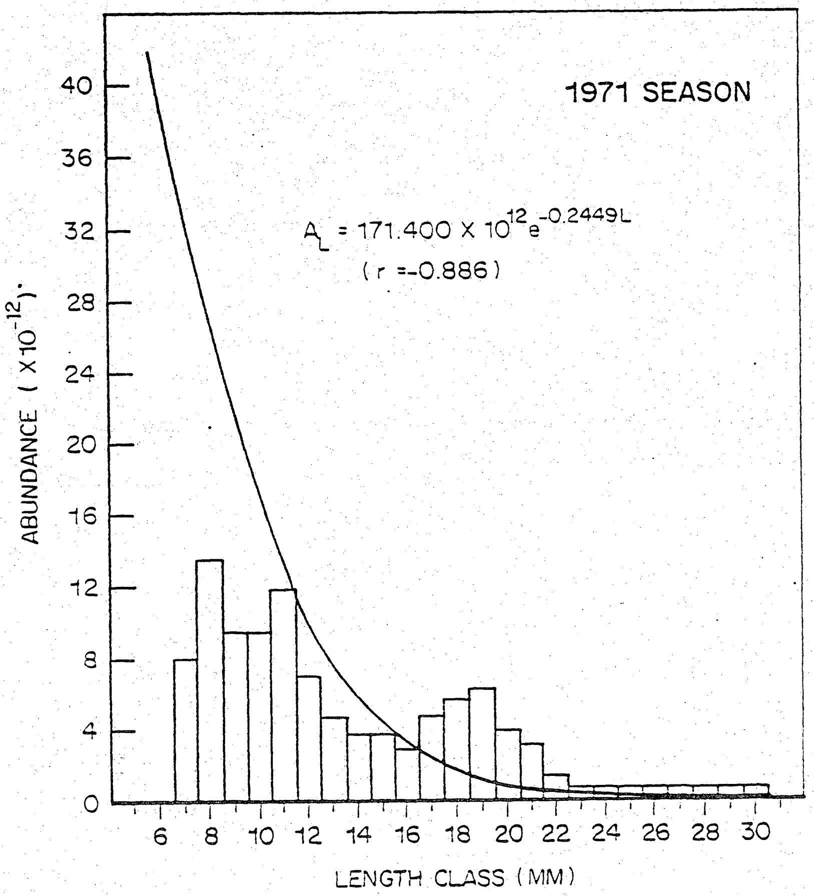

Figure 6a. Exponential regression of larval herring estimates seasonal abundance on length for 7-30-mm length classes, 1971-1978 seasons, Georges Bank - Nantucket Shoals area. The exponential curve described from the equation shown is extrapolated back to an estimated abundance at a hatch length of 5.66 mm.

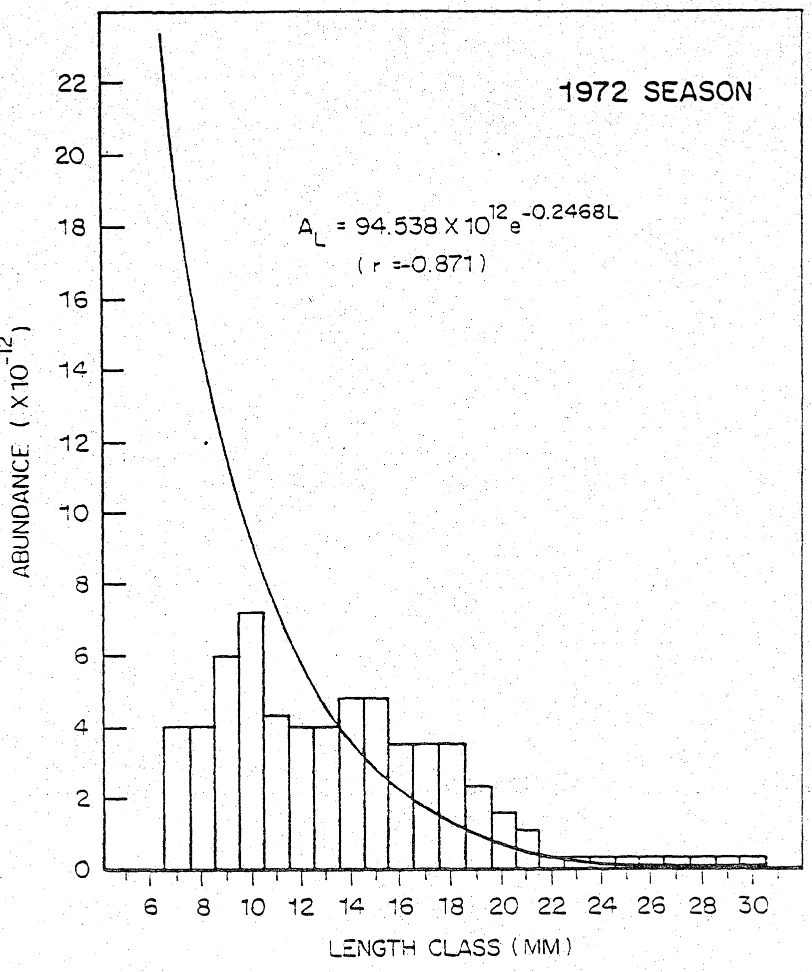

Figure 6b. Exponential regression of larval herring estimates seasonal abundance on length for 7-30-mm length classes, 1971-1978 seasons, Georges Bank - Nantucket Shoals area. The exponential curve described from the equation shown is extrapolated back to an estimated abundance at a hatch length of 5.66 mm.

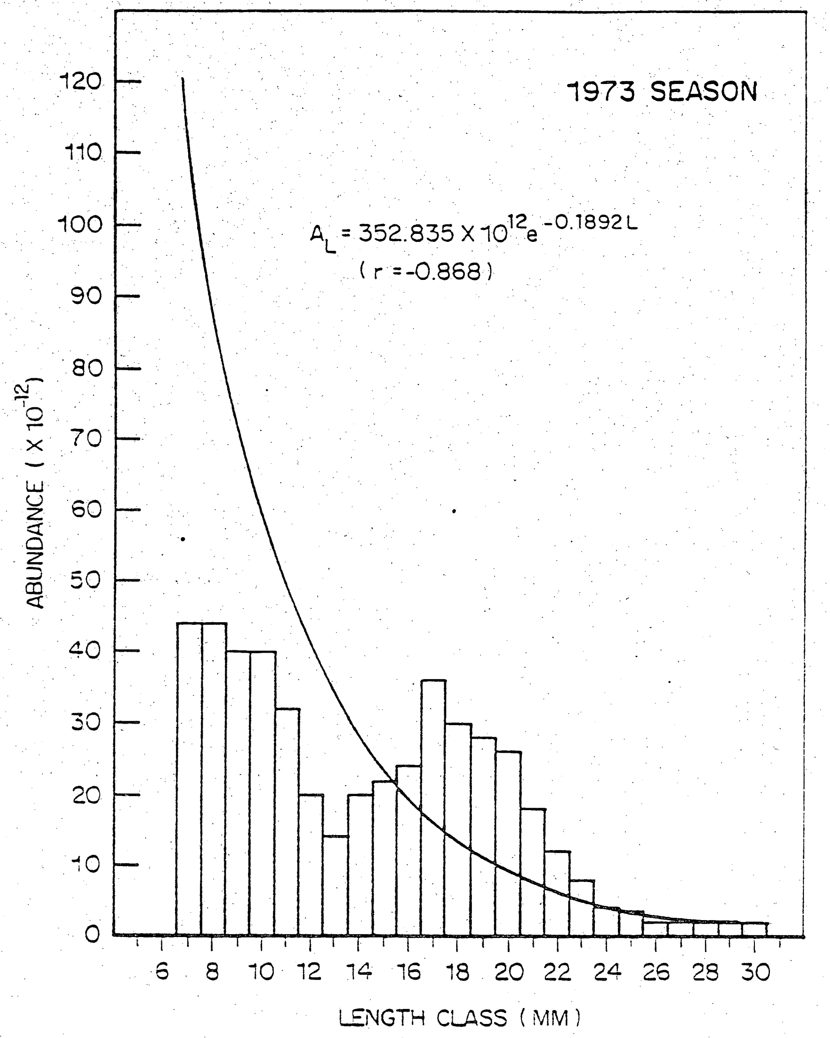

Figure 6c. Exponential regression of larval herring estimates seasonal abundance on length for 7-30-mm length classes, 1971-1978 seasons, Georges Bank - Nantucket Shoals area. The exponential curve described from the equation shown is extrapolated back to an estimated abundance at a hatch length of 5.66 mm.

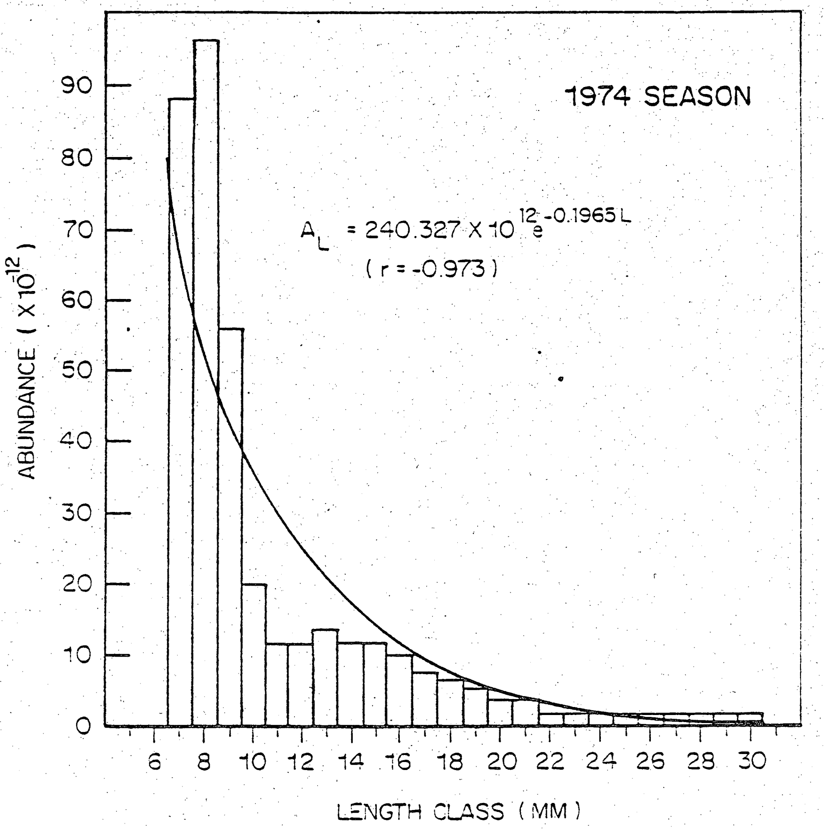

Figure 6d. Exponential regression of larval herring estimates seasonal abundance on length for 7-30-mm length classes, 1971-1978 seasons, Georges Bank - Nantucket Shoals area. The exponential curve described from the equation shown is extrapolated back to an estimated abundance at a hatch length of 5.66 mm.

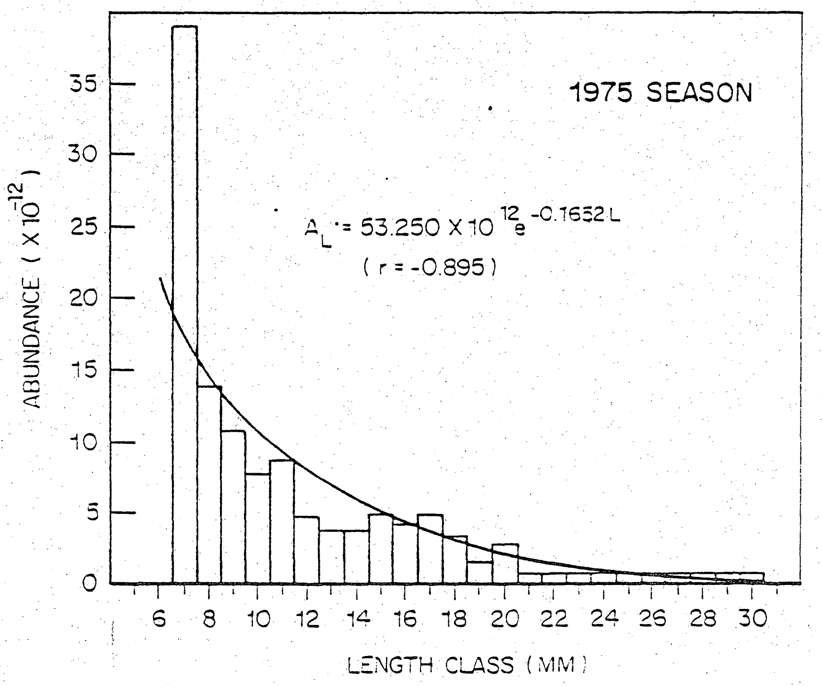

Figure 6e. Exponential regression of larval herring estimates seasonal abundance on length for 7-30-mm length classes, 1971-1978 seasons, Georges Bank - Nantucket Shoals area. The exponential curve described from the equation shown is extrapolated back to an estimated abundance at a hatch length of 5.66 mm.

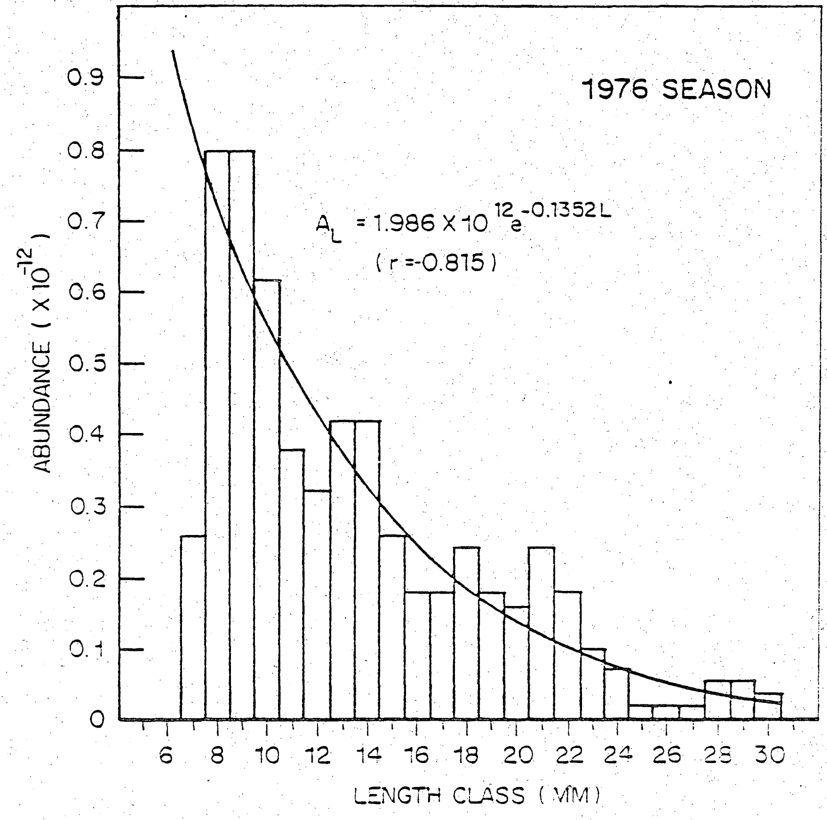

Figure 6f. Exponential regression of larval herring estimates seasonal abundance on length for 7-30-mm length classes, 1971-1978 seasons, Georges Bank - Nantucket Shoals area. The exponential curve described from the equation shown is extrapolated back to an estimated abundance at a hatch length of 5.66 mm.

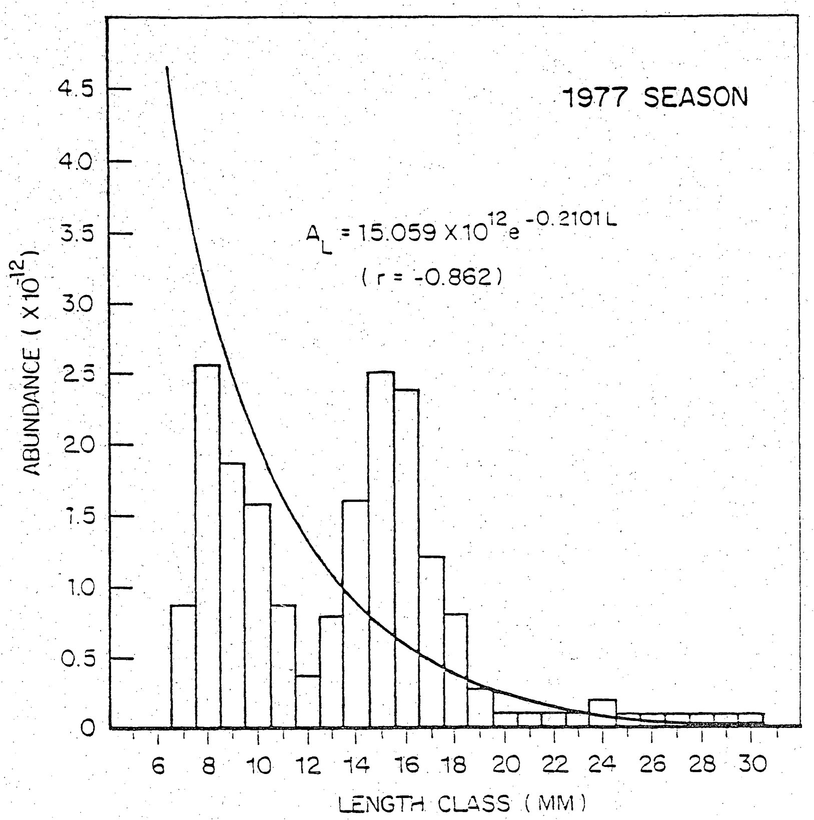

Figure 6g. Exponential regression of larval herring estimates seasonal abundance on length for 7-30-mm length classes, 1971-1978 seasons, Georges Bank - Nantucket Shoals area. The exponential curve described from the equation shown is extrapolated back to an estimated abundance at a hatch length of 5.66 mm.

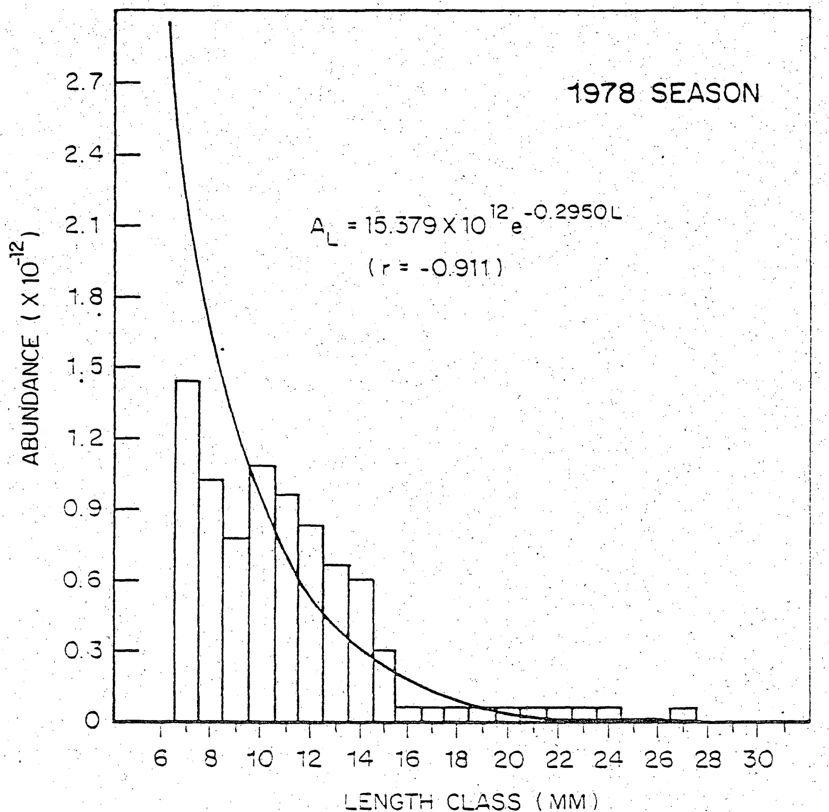

Figure 6h. Exponential regression of larval herring estimates seasonal abundance on length for 7-30-mm length classes, 1971-1978 seasons, Georges Bank - Nantucket Shoals area. The exponential curve described from the equation shown is extrapolated back to an estimated abundance at a hatch length of 5.66 mm.

APPENDIX

1971 SEASON LARVAL HERRING ABUNDANCE ESTIMATES

Length Class (mm)	c	Std. Error	Abundance (A_Lx10^{-12})
7.0	45.082	19.668	8.351
8.0	69.500	26.747	14.042
9.0	46.729	17.064	10.238
10.0	42.044	15.382	10.173
11.0	47.409	23.578	12.117
12.0	31.529	11.425	7.764
13.0	21.031	7.154	5.229
14.0	17.478	5.463	4.015
15.0	17.121	5.445	4.282
16.0	11.818	2.509	3.482
17.0	13.294	2.833	5.219
18.0	16.557	3.384	6.296
19.0	15.198	3.799	6.511
20.0	10.999	2.735	4.451
21.0	9.332	2.836	3.844
22.0	5.885	1.675	2.162
23.0	3.600	1.046	1.340
24.0	2.177	.683	.832
25.0	1.755	.530	.571
26.0	.709	.402	.147
27.0	.699	.381	.197
28.0	.360	.252	.077
29.0	.229	.177	.047
30.0	.042	.024	.013

1972 SEASON LARVAL HERRING ABUNCANCE ESTIMATES

Length Class (mm)	c	Std. Error	Abundance (A_Lx10^{-12})
7.0	21.238	10.316	4.179
8.0	21.120	7.024	4.239
9.0	28.583	8.149	6.159
10.0	35.182	9.013	7.388
11.0	21.452	5.088	4.696
12.0	18.815	4.841	4.321
13.0	17.075	3.499	4.136
14.0	19.026	3.787	4.797
15.0	21.159	4.158	5.128
16.0	13.741	2.392	3.620
17.0	14.092	2.461	3.811
18.0	13.370	2.297	3.787
19.0	9.197	1.732	2.686
20.0	5.846	1.209	1.740
21.0	3.786	.904	1.203
22.0	1.587	.412	.556
23.0	1.305	.344	.496
24.0	.572	.256	.199
25.0	.234	.098	.101
26.0	.209	.130	.104
27.0	.012	.012	.006
28.0	.186	.107	.089
30.0	.120	.087	.060

c = The mean number of larvae per 10 m^2 based on the delta-distribution.

Abundance (no. of larvae x 10^{-12}) is c expanded by cruise durations and the study area size (99750 km^2).

1973 SEASON LARVAL HERRING ABUNDANCE ESTIMATES

Length Class (mm)	c	Std. Error	Abundance ($A_L \times 10^{-12}$)
7.0	223.795	84.385	45.010
8.0	218.309	93.651	45.290
9.0	193.998	81.921	41.661
10.0	194.638	71.684	41.138
11.0	155.139	47.047	32.094
12.0	101.818	26.142	21.862
13.0	72.202	16.071	15.804
14.0	93.827	25.737	21.265
15.0	89.430	20.348	22.136
16.0	92.508	18.697	24.598
17.0	129.412	26.504	37.916
18.0	96.073	18.781	31.035
19.0	92.349	23.066	28.938
20.0	77.879	17.353	27.289
21.0	49.933	11.660	19.292
22.0	33.384	7.666	13.552
23.0	23.141	6.032	8.706
24.0	14.764	3.514	5.735
25.0	9.396	2.630	4.049
26.0	3.733	1.155	1.521
27.0	1.801	.720	.812
28.0	1.250	.466	.525
29.0	1.063	.453	.507
30.0	1.329	.657	.623

1974 SEASON LARVAL HERRING ABUNDANCE ESTIMATES

Length Class (mm)	c	Std. Error	Abundance ($A_L \times 10^{-12}$)
7.0	437.828	300.473	89.776
8.0	478.976	335.705	97.876
9.0	280.102	187.577	57.143
10.0	106.812	46.575	21.980
11.0	58.043	16.567	13.172
12.0	51.470	12.590	13.362
13.0	49.558	10.846	14.113
14.0	43.846	8.169	12.890
15.0	51.469	10.207	12.959
16.0	43.526	9.202	10.406
17.0	36.706	7.187	9.409
18.0	29.911	6.086	8.054
19.0	20.044	4.143	6.247
20.0	19.830	5.503	7.284
21.0	10.830	2.681	4.071
22.0	10.480	3.048	4.266
23.0	6.018	2.056	2.603
24.0	3.283	1.098	1.514
25.0	3.811	1.355	1.737
26.0	2.351	.829	1.051
27.0	3.336	1.667	1.515
28.0	2.673	.936	1.193
29.0	1.570	.564	.707
30.0	1.501	.625	.671

c = The mean number of larvae per 10 m^2 based on the delta-distribution.

Abundance (no. of larvae x 10^{-12}) is c expanded by cruise durations and the study area size (99750 km^2).

1975 SEASON LARVAL HERRING ABUNDANCE ESTIMATES

Length Class (mm)	c	Std. Error	Abundance ($A_L x 10^{-12}$)
7.0	217.282	146.298	39.718
8.0	70.026	30.161	14.027
9.0	50.061	16.151	11.013
10.0	41.304	11.772	8.933
11.0	43.539	13.595	9.137
12.0	22.411	5.192	5.031
13.0	17.388	3.821	4.303
14.0	16.325	3.701	4.402
15.0	18.298	4.358	5.229
16.0	14.229	3.254	4.336
17.0	14.786	2.521	5.034
18.0	7.660	2.296	3.770
19.0	7.707	1.479	2.992
20.0	7.611	1.653	3.000
21.0	4.208	.927	1.799
22.0	2.297	.573	.969
23.0	1.055	.265	.486
24.0	.628	.200	.291
25.0	.786	.206	.357
26.0	.915	.240	.403
27.0	1.521	.345	.662
28.0	1.794	.412	.778
29.0	1.654	.436	.710
30.0	3.705	1.028	1.589

1976 SEASON LARVAL HERRING ABUNDANCE ESTIMATES

Length Class (mm)	c	Std. Error	Abundance ($A_L x 10^{-12}$)
7.0	2.365	1.208	.271
8.0	6.298	3.507	.800
9.0	5.514	2.303	.798
10.0	4.673	2.190	.641
11.0	2.838	1.226	.384
12.0	1.614	.399	.340
13.0	1.912	.440	.432
14.0	1.766	.452	.423
15.0	1.108	.249	.260
16.0	.816	.218	.186
17.0	.758	.189	.187
18.0	.881	.152	.246
19.0	.753	.183	.192
20.0	.612	.152	.168
21.0	.942	.362	.245
22.0	.725	.278	.189
23.0	.378	.160	.109
24.0	.374	.203	.094
25.0	.055	.035	.025
26.0	.010	.010	.005
27.0	.102	.059	.042
28.0	.150	.087	.065
29.0	.170	.072	.074
30.0	.124	.057	.053

c = The mean number of larvae per 10 m^2 based on the delta-distribution.

Abundance (no. of larvae x 10^{-12}) is c expanded by cruise durations and the study area size (99750 km^2).

1977 SEASON LARVAL HERRING ABUNDANCE ESTIMATES

Length Class (mm)	c	Std. Error	Abundance ($A_L x 10^{-12}$)
7.0	4.052	3.067	.991
8.0	10.974	8.308	2.683
9.0	7.766	6.324	1.901
10.0	6.792	5.218	1.665
11.0	3.568	2.322	.896
12.0	1.408	.386	.423
13.0	2.642	.811	.846
14.0	5.067	1.585	1.617
15.0	8.127	2.517	2.593
16.0	7.853	1.957	2.468
17.0	3.848	1.036	1.228
18.0	2.574	.719	.831
19.0	.893	.252	.306
20.0	.334	.117	.128
21.0	.146	.076	.057
22.0	.226	.105	.111
23.0	.374	.157	.160
24.0	.462	.240	.228
25.0	.126	.062	.063
26.0	.131	.064	.065
27.0	.262	.127	.131
28.0	.042	.024	.021
29.0	.011	.011	.005
30.0	.078	.056	.039

1978 SEASON LARVAL HERRING ABUNDANCE ESTIMATES

Length Class (mm)	c	Std. Error	Abundance ($A_L x 10^{-12}$)
7.0	7.264	2.784	1.480
8.0	5.292	1.952	1.031
9.0	3.851	1.372	.825
10.0	4.748	2.084	1.093
11.0	4.058	1.767	.955
12.0	3.723	1.591	.853
13.0	2.971	1.314	.686
14.0	2.710	1.479	.628
15.0	1.282	.635	.319
16.0	.042	.024	.018
17.0	.055	.027	.024
18.0	.104	.067	.052
19.0	.103	.060	.048
20.0	.105	.053	.049
21.0	.088	.049	.044
22.0	.086	.047	.043
23.0	.079	.052	.040
24.0	.012	.012	.006
27.0	.012	.012	.006

c = The mean number of larvae per 10 m^2 based on the delta-distribution.

Abundance (no. of larvae x 10^{-12}) is c expanded by cruise durations and the study area size (99750 km^2).