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Abundance and Survival of Sea Herring (*Clupea harengus* L.) Larvae  
in Relation to Environmental Factors, Spawning Stock Size, and  
Recruitment for the Georges Bank Area, 1968-1977 Seasons\*

by

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## 1. INTRODUCTION

Surveys of Atlantic larval herring (*Clupea harengus harengus* L.) have been conducted in the Gulf of Maine - Georges Bank area 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, Legaré, Scattergood, and Temple 1958; Tibbo and Legaré 1960; Colton, Honey, and Temple 1961; Marak and Colton 1961; Marak, Colton, and Foster 1962; Marak, Colton, Foster, and Miller 1962). Spawning occurs predominantly in the autumn in the shoal areas of Georges Bank, Southwestern Scotian Shelf (Das 1968), and Western Gulf of Maine (Graham, Chenoweth, and Davis 1972). Boyar, Marak, Perkins, and Clifford (1973) have summarized the seasonal distribution of larval herring in the Georges Bank - Gulf of Maine area 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 in press). 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 size over a wide range of stock sizes (see Postuma and Zijlstra 1975), 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 in press). Interest in conservation of this stock and the general belief in the hypothesis that success of a year class of marine fish is controlled by factors operating during the larval stage led the International Commission for the Northwest Atlantic Fisheries (ICNAF) to develop a major cooperative research program on the early life history of sea herring in the Georges Bank - Gulf of Maine area. ICNAF larval herring surveys began in autumn 1971 and were designed to measure major variations in larval production, dispersal, growth, and mortality between spawning seasons and areas with the long-term objective of identifying mechanisms controlling larval survival in the first 6 months, or at least environmental conditions associated with large and small year classes. In this paper we present the analyses completed to date of the larval herring data base for the Georges Bank - Nantucket Shoals area, which include estimates of 1968-77 larval production in relation to spawning stock size, average growth and mortality rates, and a comparison of these parameters with available data on recruitment. Also we summarize our present findings on environmental factors that may affect larval survival by examining available data on the possible loss of larvae from the banks, the abundance and distribution of larval food prey organisms, and suspected competitors and predators. The results reported here are based primarily on the 0.505-mm mesh samples; future analyses of the time series are to be made on total ichthyoplankton and zooplankton from the 0.333-mm samples.

## 2. SAMPLING METHODS

Vessels and cruise dates listed in Table 1 comprise the 37 surveys used in this study of larval herring in the Georges Bank - Nantucket Shoals area, 1968 through the 1977 spawning seasons. The sampling design, gear, and towing profile have been modified somewhat during this time and the various methods can be grouped into four periods: (1) the groundfish-plankton surveys 1968-70, (2) initial ICNAF larval herring surveys of 1971, (3) ICNAF surveys using standard tow profile beginning with the 1972 season, and (4) concentration of sampling effort in the Georges Bank - Nantucket Shoals area since the 1975 season.

Between 1968 and 1970, plankton hauls were made on groundfish surveys (stratified-random design) conducted each autumn in the Georges Bank - Gulf of Maine area by the National Marine Fisheries Service (NMFS), Northeast Fisheries Center (NEFC). A 20-cm bongo sampler (0.505-mm mesh nets) was hauled at 3.5 knots (6.5 km/h) in a step-oblique manner. Only a surface tow of 5-15 min was made in water less than 27 m. In water greater than 27 m, a step-oblique tow

was made to a depth of 40-55 m with 3- or 5-min steps at 50 m, 25 m, and surface. Although this data is questionable and fragmentary, we have included it in our analyses as an order-of-magnitude estimate of larval production at a time when the spawning stocks were still at a moderately high level.

When the ICNAF larval herring surveys were initiated in 1971, the approach was to cover the entire Georges Bank - Gulf of Maine with a standardized grid of sampling stations 15-20 miles apart at least once a month from September through December (Figure 1). At each station a 3.5-knot double-oblique tow was made using a 61-cm bongo sampler (0.505- and 0.333-mm mesh). The gear configuration is described in Smith and Richardson (1977, p. 20). The net 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 June 1974 the newly formed ICNAF Environmental Working Group recommended more intensive studies of factors controlling the recruitment process. In February 1974 the USA began a series of February surveys to examine the overwinter picture. Small bongo samplers (20 cm) with fine mesh were added to the 60-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.

Each country generally was responsible for sorting and measuring herring larvae from their 0.505-mm mesh samples and reporting the standardized results for the annual ICNAF assessment meetings and summaries submitted as ICNAF Research Documents. Despite protocols to standardize the laboratory processing of samples, various length conventions have been used in measuring larvae and subsampling methods by the participants. This problem and its effect on length-frequency distributions was considered by Lough (1976b). Most of the 0.505-mm mesh larval herring measurements used in this study represent standard length (SL) to the nearest mm. Cruises using other measurement conventions have been corrected to SL, nearest mm, based on regression relationships from the literature. Differences in the corrected length-frequency data probably lie within  $\pm 0.5$  mm. Only the 0.505-mm mesh, 61-cm bongo samples were used in this study, except for the three ALBATROSS IV cruises for the 1968-70 seasons where a 20-cm bongo was used, and for the ANTON DOHRN 77-03 and ALBATROSS IV 78-02 cruises where only the 0.333-mm mesh samples were sorted. Further analysis will be made on all 0.333-mm mesh samples, zooplankton as well as ichthyoplankton, and selected samples of the fine mesh for the smaller plankton. More detailed information concerning cruise and station data as well as the various methods used can be found in Lough and Bolz (1979a,b).

### 3. LARVAL ABUNDANCE, GROWTH, AND MORTALITY ESTIMATES

#### 3.1 Methods

Larval herring catches were first standardized to numbers per  $m^2$  by 1-mm length classes, expanded to the rectangular area ( $1.16 \times 10^9 m^2$ ) represented by each station, and all station area abundances summed to estimate total cruise abundance. These preliminary cruise abundance totals by 5-mm size classes are provided in Table 2 for the 1968-77 seasons, Georges Bank - Nantucket Shoals area.

A number of different methods have been used to estimate seasonal larval abundance, partly for comparative purposes, but also because some of the survey data is so limited that only one method was appropriate to use. The various methods are referred to as: (1) the normal curve approximation method of Saville (1956), (2) the integrated polygon method of Simpson (1959), and (3) the expanded day and area method of Sette and Ahlstrom (1948) incorporating a stage duration correction. General formulas and assumptions for these three techniques have been outlined recently by Houde (1977a).

Saville (1956) Method. The method of Saville (1956), modified by Houde (1977a), can be used to estimate seasonal larval abundance within an area from single or multiple cruises if the seasonal spawning (hatching) intensity approximates a normal curve. Each cruise period within the hatching season in the case of herring therefore would represent some portion of the curve. To estimate the initial abundance of larvae by this method, the length and peak of the hatching season must be known. Total abundance of larval herring less than 10 mm (4-9-mm size classes) from a cruise was first plotted on a log scale against time for each season. The standard length of Formalin-preserved herring larvae at hatch falls within the 4-6-mm size classes. A composite hatching curve could be drawn for the 1971-77 seasons, where 3-5 cruises covered the area sufficiently in time, that closely approximates a log-normal curve with a slight skewness on the right-hand side of the curve. This skewness results from the fact that hatching of larvae from spawning grounds in the more southerly Nantucket Shoals area always follows that of the northern Georges Bank area in time by 1-2 weeks. The length and middates of the 1968-70 seasons were based upon the average date of the 1970-73 seasons as there is some indication that the onset of spawning occurred later in the season in more recent years. The total initial larval abundance was calculated for each season by the normal curve approximation method using individual cruise abundance estimates. Where multiple cruises occurred within the same season, the independent cruise estimates were combined to yield arithmetic and geometric means, and confidence limits estimated.

Simpson (1959) Method. When several cruises bracket a spawning season, the Simpson (1959) method can be used to estimate initial larval abundance instead of assuming the normal curve approximation. Abundance of larvae less than 10-mm length from each cruise area was plotted against their cruise middates. The points were connected, and the area integrated under the polygon estimated the season's initial larval abundance. This quick and simple method was used to calculate initial estimates of the initial abundance of recently hatched larvae for the 1971-77 seasons for timely ICNAF reports.

Sette and Ahlstrom (1948) Method. Sette and Ahlstrom (1948) developed a technique for computing the duration and age of each size class if an accurate growth rate is known. Duration corrected abundance plotted against the mean age of a size class also can be used to estimate larval mortality. Growth of larval fish is generally expressed in terms of length rather than weight as length measurements are more readily available. Many studies have provided general rates of larval growth and shape of the curve, but as yet the precise form of growth curves for field-caught herring larvae from hatching (4-6 mm) to metamorphosis (-49-55 mm, see Boyar et al. 1973) has not been made. It is especially important to be able to incorporate seasonal and geographical variations in population growth if one is to accurately estimate larval abundance and compare survival curves. Growth patterns of various clupeid-like larval fish have been described as logarithmic (exponential curve plotted on an arithmetic scale) in some studies by Marshall, Nicholls, and Orr (1938), Sette (1943), Ahlstrom (1954), Farris (1961), Nakai and Hattori (1962), and Houde (1977a,b,c). Marshall, Nicholls, and Orr (1938) concluded that two logarithmic curves with a change in slope at a length of about 19 mm provided a better description of larval herring growth. Subsequent studies from field data on the eastern side of the Atlantic have borne out the nonlinear nature of larval herring growth based on length. A decrease in growth after about 20 mm was shown by Graham, Chenoweth, and Davis (1972, p. 313) for herring larvae collected along the coastal Gulf of Maine during the autumn. Sameoto (1972, p. 510) used a parabolic function to describe larval herring growth through the autumn, winter, and spring in St. Margaret's Bay, Nova Scotia. A Gompertz-type curve may best describe the decaying exponential growth pattern (Zweifel and Lasker 1976).

Following the method of Sette and Ahlstrom (1948) and using the notation of Houde (1977a), an instantaneous growth coefficient,  $g$ , was calculated as follows:

$$g = \frac{\log_e L_t - \log_e L_0}{t}$$

where  $L_0$  = minimum length of larvae (6.5 mm, the lower limit of the 7-mm size class). Our findings indicate that yolk sac resorption is fairly complete about 5 days post-hatching (10°C) at a modal length of 7 mm.

$L_t$  = maximum length of larvae considered assuming exponential growth (30.4 mm, the upper limit of the 30-mm size class).

$t$  = time to grow from  $L_0$  to  $L_t$  at a mean daily growth increment of  $\bar{b}$  (mm/day),

$$\text{where } t = \frac{L_t - L_0}{\bar{b}}$$

An average  $\bar{b}$  value of 0.195 mm/day ( $g = 0.0126$ ) was used in the exponential growth model as the best compromise to describe average growth from October through February in this study. The time to grow from 6.5 to 30.4 mm at 0.195 mm/day using the exponential model takes 123 days, which agrees with the field data on the time to grow from recently hatched larvae in October to a modal size of about 30 mm in February. A wide range of  $\bar{b}$  values have been reported in the literature for premetamorphosing herring larvae and calculated from the field data in this study. Generally the values range from about 0.13 to 0.35 mm/day with an average of 0.20 mm/day. Growth values tend to be higher for larvae less than 20-mm length and lower for larvae greater in length. The  $\bar{b}$  value of 0.195 mm/day used in this study was derived from a number of corroborative methods. If larvae collected on surveys during the autumn are assigned a  $\bar{b}$  of 0.22 mm/day based on lab-reared larvae (Ehrlich, Blaxter, and Pemberton 1976), and larvae collected during the December-February period were found in this study to have an average  $\bar{b}$  of 0.17 mm/day, then the overall average for the first 6 months results in 0.195 mm/day. Also, the same growth average can be obtained by averaging various points of the Gompertz curve fitting to length versus age of larvae based on preliminary otolith-aging techniques (unpublished data).

A computer program was used to calculate the duration ( $D_t$ ) of each 1-mm larval length class by the formula:

$$D_t = \frac{\log_e L_B - \log_e L_A}{g}$$

where  $L_B$  is the upper boundary of the size class

$L_A$  is the lower boundary of the size class

$g$  is the instantaneous growth defined previously.

Larvae in the 4-6-mm length class (size at hatching) were assigned a duration of 10.3 days.

The average age ( $T_A$ ) of each length class from hatching ( $T_0$ ) was calculated by the following formula and summed from time zero ( $T_0$ ):

$$\begin{aligned} T_A &= \text{duration of 4-6-mm length class (5.06 days)} \\ &+ \text{duration of successive length classes} \\ &+ \frac{\log_e L_b - \log_e L_a}{g} \end{aligned}$$

where  $L_b$  is the length-class midpoint

$L_a$  is the smallest size larvae considered (6.5 mm)

$g$  is defined above.

The estimated abundance values are then corrected by dividing each size class by its duration. An example of the computer output is provided in Table 5. Using this method, an estimate of the seasons' total initial production of larvae was made by summing the 4-9-mm size class duration-corrected abundances to allow for missing the very early size classes within and between surveys.

An average seasonal mortality estimate then was computed from the exponential regression of duration-corrected abundances against mean ages to obtain the instantaneous mortality coefficient ( $Z$ ) as well as the  $Y$ -intercept value as another estimate of initial larval abundance. Larvae in the 4-6-mm size class were always underrepresented in the samples and therefore were not considered in the mortality estimation. The average mortality rate obtained in this manner could then be used to adjust the duration-corrected abundance of larvae less than 10-mm length to provide a better estimate of the initial production, assuming a constant mortality of these early stages was similar to the average seasonal rate. These details are footnoted in Table 7.

### 3.2 Sources of Error

Estimates of the various sources of error from egg and larval surveys and a discussion of the reliability and assumptions in the methodology used in this paper have been made by Sette (1943), Sette and Ahlstrom (1948), Ahlstrom (1954), Taft (1960), Saville (1956, 1964), English (1964), Harding and Talbot (1973), Houde (1977a,b,c), and others. Saville (1956) partitions the three main sources of error as those associated with the individual sample collection, the integration of sample estimates over the cruise area, and the cruise total estimates over time. The integration of cruise totals over the spawning season is generally regarded as the most serious source of error. Most of the errors in abundance estimates have been made on the nonmotile eggs where one might expect variance estimates to be smaller than those for the larvae due to avoidance problems. However, Harding and Talbot (1973) found for plaice that the 95% confidence intervals of the mean seasonal abundance estimates were smaller for the larval than the egg stages which may be a result of the more patchy distribution of newly spawned eggs. The 95% confidence limits are generally regarded as half or double the estimate (Saville 1964). Confidence limits of the mean seasonal estimates may be narrower than for individual samples within a cruise.

Some preliminary estimates of error have been made in this paper from the larval herring survey data, 0.505-mm mesh samples, but mostly on grouped data rather than individual station data. A more rigorous analysis will be made in the future using the 0.333-mm mesh samples, which will eliminate the subsampling and measurement inconsistencies of the 0.505-mm samples and reduce errors associated with possible extrusion through the coarser mesh. Some indication of the precision in estimates of larval production can be obtained from the standard deviations of estimates of mean numbers of larvae on a per-cruise basis. Data for the eastern Georges Bank spawning site were summarized for two size categories (5-10 mm, 10-15 mm) on all cruises from September through December 1972-76. There were 37 standard stations occupied on each cruise in the area from 68° west longitude to the eastern edge of Georges Bank (Figure 1). Means, standard deviations, and coefficients of variation (CV) for each larval size category and cruise are presented in Table 3. For the 5-10-mm length group, CV's range from 2.7-5.5 with a mean of 3.8, and comparable values of CV for the 10-15-mm group were 1.7-4.0 with a mean of 2.6; CV's for cruises with means ( $\bar{X}$ ) less than or equal to 1 are not included in these ranges or mean values of CV. Although these CV's are large, they are not so large as to obscure the very large differences in larval production which have occurred on Georges Bank since 1971. Another encouraging feature is the fact that within a given season the mean 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 one place.

Another measure of variability which is of interest here was derived from a 1974 study of vertical distribution of herring larvae on Georges Bank. A series of simultaneous horizontal tows were made at 6 depths, every 2 hours for 40 hours, at a single location on Georges Bank in a concentration of recently hatched herring larvae. A total of 21 hauls were made and the CV's of mean larval densities (no./100m<sup>3</sup>) for the 6 depths ranged from 0.6 to 1.6,

with a mean of 0.9. The CV for the estimated mean abundance per 10m<sup>3</sup> (integrated over the water column) was 0.6. This level of within-station variability is not too large to obscure major differences in vertical distribution of larvae and is small enough so that one can place reasonable confidence in a single oblique haul such as one of the standard ICNAF hauls. That is, the implication here is that a grid pattern such as that used in the ICNAF program is adequate to detect major differences in larval distribution and abundance. However, it is also clear that because of the highly skew distribution, significant improvements in precision on a per-cruise basis would require a very large increase in density of stations. If it becomes necessary to achieve higher precision of abundance estimates, it would be more effective to increase the frequency of cruises rather than the density of stations per cruise. It is obvious that certain types of studies (e.g., short-term phenomena such as dispersal vs currents, larval feeding and mortality vs densities of zooplankton and as predators within a larval patch) will require much more intensive sampling in time and space to produce definitive results.

Survey coverage of the Georges Bank - Nantucket Shoals area has not been entirely adequate in all years. The shoal waters, less than about 25 m, of Nantucket Shoals have not been sampled, and at times the surveys have not been able to extend their coverage far enough off the southern edge of the shelf and the most western limit of the area to encompass the larval population. Except for the inshore Nantucket Shoals area, the sampling coverage for the Georges Bank - Nantucket Shoals area has been remarkably good since 1971. However, the 1976 surveys appear to have missed some of the small larvae less than 10 mm, and the 1971 surveys' towing profile would lead us to believe that abundance of all larvae in shoaler areas would be underestimated. If we are missing a significant portion of the inshore Nantucket Shoals recently hatched larvae, which later enter the sampling area, then the effect would be to underestimate the abundance of the initial size classes, thus underestimating the seasonal average mortality rate for the combined Nantucket Shoals - Georges Bank assessment, and especially so in years when spawning is predominantly on Nantucket Shoals rather than on Georges Bank.

Extrusion of small larvae through the mesh and escapement of large larvae are two possible sources of errors in the larval herring sampling. Extrusion can be a significant problem for the retention of relatively small organisms, especially at high towing speeds (Smith and Richardson 1977). Theoretical measurements of larval herring skull widths vs the mesh diagonal indicate that minimum lengths for complete retention could be 9.0 and 7.5 mm for 0.505- and 0.333-mm mesh, respectively (Colton and Green 1975). The extent of extrusion of the small larvae has not yet been estimated adequately from the samples. Graham and Chenoweth (1973) found no evidence of extrusion of recently hatched herring larvae (4-9 mm) through mesh sizes of 0.253, 0.333, 0.366, and 0.505 mm made from high-speed tows (5 knots). Abundance estimates made in this paper indicate clearly that most of the 4-6-mm larvae are extruded from 0.505-mm mesh. The extrusion of small larvae is only one source of bias in estimates of recently hatched herring larvae; another is the fact that samplers do not get closer than 5 m to the bottom and thus may miss the smallest-size larvae as noted by Colton and Green (1975) and Wood (1975).

The size of herring larvae at which significant escapement occurs from the 61-cm bongos at 3.5 knots occurs has not been determined. Analysis of day/night catches so far has not provided any significant diel differences during the first 6 months. Escapement does not appear to be a major problem even as late as March, but some day/night adjustment probably will be made when all the data are analyzed. The larval herring towing speed of 3.5 knots is a compromise between slow hauls to minimize extrusion of small larvae and fast hauls to minimize escapement of larger larvae.

The Sette and Ahlstrom (1956) method of estimating larval abundance and survival curves required some knowledge of the form of the larval growth curve. In this paper an exponential growth curve was used because a more definitive growth model is lacking. A wide range of growth coefficients was estimated from the field data by attempting to follow homologous length modes from cruise to cruise. This method has limited reliability due to the subjectivity of choosing homologous modes and the extended length of the spawning season. Average rates of growth can be determined by this method, however, and it provides a relative means of studying cohorts of larvae over time in the absence of finer-scaled surveys. Precise larval growth estimates could

not be obtained from the polymodal length-frequency data to compare rates between seasons or areas, especially during the autumn, so that the same seasonal average growth estimate was used for all years. Variations in cohort growth would alter the duration-corrected abundance estimates and seasonal mortality rates. Farris (1960) discusses the effect of form of the growth estimates of larval fish survival. If the larval herring growth curve over the first 6 months of life is more of a convex Gompertz type, then the concave exponential growth curve used in this study would tend to overestimate the duration of the size classes initially, perhaps by twice the number of days, thus underestimating the corrected abundances by a factor of two. This seems to be the case for larvae less than 15 mm in length. On the other hand, larvae greater than 25 mm in length may be overestimated as their stage duration is longer according to the Gompertz growth curve than predicted by the exponential curve. In effect, the exponential growth curve would underestimate mortality if in fact the growth curve was more convex.

### 3.3 Results

Survey coverage of the Georges Bank - Nantucket Shoals spawning beds and spread of larvae was virtually complete from September through December for the 1971 and 1972 seasons, and from September through February for the 1973 through 1977 seasons. Table 2 shows a fairly even progression in larval abundance by size classes from cruise to cruise each season. The average length of the hatching season, 1971-77, was 96 days, from 19 September through 24 December (Table 4) with an average Julian middate of 6 November (3-day standard deviation) and an average weighted middate of 25 October (6-day standard deviation). The data indicate that the onset of the spawning (hatching) season occurred progressively later in the time series, ranging from mid-September - mid-October in the 1971-73 seasons, to late October - first part of November in recent years. Peak early maturation time of herring on Georges Bank has been correlated with warm bottom temperatures in August by Berenbeim and Sigaeu (1978). However, there appears to be a different relationship between the spawning time and water temperatures based on the larval herring data vs autumn bottom water temperatures. Davis (1978a,b) reported that average bottom water temperatures on Georges Bank (reference date 7 November) have been increasing since the late 1960's through 1977, and during that period reached peak values in 1973, 1974, 1976, and 1977. At the same time we have observed, with the exception of 1973, that the onset of hatching has been significantly later in these warmer years (Table 4), suggesting that the delayed spawning may have been related to the warmer autumn temperatures. However, another factor which may have contributed to delayed spawning in some recent years is the shift of major spawning activity from eastern Georges to western Georges and Nantucket Shoals area where spawning traditionally is later by at least 1-2 weeks. Finally, there is the possibility that the shift in the spawning seasons 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 stocks. 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.

Initial larval abundance estimates for the 1968-77 seasons by the various methods used are presented in Tables 4, 6, and 7. The range of estimates among the methods falls within one to two orders of magnitude, about as wide as the 95% confidence limits computed for some of the estimates. However, the ranking of the seasonal initial abundance estimates remains essentially the same by whichever method used. Therefore, the relative size of each season's estimates represents a true picture in most cases. The mortality and duration-corrected abundance estimates by the methods of Sette and Ahlstrom (1948) and Saville (1956) are believed to be the best estimates of initial larval production for the 1971-77 seasons. Estimates from both methods are quite similar, but the Sette and Ahlstrom method estimates are consistently higher than the Saville estimates. Production of larvae in the combined Georges Bank - Nantucket Shoals area was highest for the 1973 and 1974 seasons, an order of magnitude lower in 1972 and 1975, low for the 1971 and 1977 seasons, and extremely low in 1976. The extremely low 1976 season estimate may have been an underestimate by as much as an order of magnitude due to survey timing and relatively wide station spacing. Raising the 1976 season estimate of larvae less than 10-mm length would bring it more in line with the abundance of larger-size larvae caught later in the season (see Figure 2).

The initial abundance of larvae for the 1968-70 seasons was estimated from single surveys each year by the normal curve approximation method. These estimates are fairly low compared to estimates for more recent years; the estimate for 1970 which was a strong year class appears to be greater than that of the 1968 and 1969 seasons but the estimates for all three years are believed to be low. The cruise middate for all three surveys falls within one standard deviation of the mean Julian date so that they adequately represent the peak of hatching. The length frequency summaries for each year also appear similar to those at the same time on other ICNAF surveys; however, only one major length mode appears in the 1968-70 data whereas multiple modes occur in more recent years. The survey coverage during 1968-70 covered approximately the same Georges Bank - Nantucket Shoals area, but the stratified-random station spacing left large gaps in some key areas and may have missed important hatching aggregations. Because of the station spacing, the single cruise coverage, and possible avoidance of the smaller bongo sampler used, the 1968-70 season's larval abundance estimates may have been underestimated by one to two orders of magnitude.

A comparison of initial larval abundance for the separate spawning areas of Georges Bank and Nantucket Shoals is given in Table 7. Production of larvae was greater on Georges Bank than Nantucket Shoals 6 out of 10 years. Larval production was greater on Nantucket Shoals during the years 1972, 1975, and 1977. Production of larvae between the two subareas was most equal during 1973, the highest seasonal production in the time-series, but the usual situation is for production to be predominantly higher in one subarea than the other. Larvae originating from separate spawning populations in these subareas early in the season are dispersed and intermixed by late autumn.

Average mortality rates were determined for two periods (autumn, autumn-winter) within each of the 1971-77 seasons by the exponential regression of duration-corrected abundance against estimated mean age in days (Table 6). Larval mortality rates during the first 6 months were typically 3-5% per day. All the regressions were significant except for the 1976 season as production of larvae was too low to measure adequately. The decline in numbers of larvae throughout the 1976 season appeared minimal so that a zero mortality coefficient was assigned. Excluding the 1976 season, the lowest autumn mortality rate of about 3% per day occurred during the 1971 and 1977 seasons when production was relatively low. The highest autumn mortality of about 5% per day occurred during 1975, a season of intermediate larval production, and it is interesting to note that the subsequent winter mortality must have been very low as the autumn-winter mortality rate for the 1975 season was among the lowest of the five autumn-winter periods.

A composite picture of the decline in larval abundance with time for the 1971-77 seasons is shown in Figure 2. Population decline does not appear to take effect significantly until after December each year. By February, larval abundance reaches a low level in all years except for the 1975 season, and perhaps the 1976 season as well. The overwinter period was examined in more detail in hopes of gaining some insight into the mortality processes. Various mortality and growth rates were estimated by the methods of Lough (1976b) in Table 8, for larvae collected during five winters, 1973-74 through 1977-78. The December larval abundance was higher in 1973 and 1974, intermediate in 1975, and low in 1976 and 1977. However, abundance of larvae in February varied reflecting the range in mortality rates from essentially zero to 5% per day. February 1976 has the greatest abundance of larvae of any February and therefore the 1975-76 winter showed a "0" instantaneous mortality rate. The 1973-74 and 1974-75 winter had the highest mortality of 4-5% per day whereas the 1976-77 and 1977-78 winters had low mortality of 1% per day or less. Larval mean length was progressively larger each February through the time series in spite of the later spawning, with the greatest growth occurring during the 1975-76 and 1974-75 winters and the lowest during the 1973-74 and 1977-78 winters.

#### 4. INDIVIDUAL COHORT GROWTH AND MORTALITY ESTIMATES

An attempt was made to delineate cohorts of larvae spawned from the same spawning area and time and follow between cruises for more refined larval growth and mortality estimates. Contour maps delineating areas of abundance by 5-mm length classes were constructed in such a manner that younger size classes of larvae from one cruise were compared to the succeeding older size

classes of larvae on the following cruise using the same procedure as Bumpus (1976) to provide a general picture of dispersion and advection. It was hoped that distinct cohorts of larvae would be highlighted by this method; however, the resolution was poor because of the relatively long time between cruises and broad station spacing. Thus, cohort growth and mortality were estimated between cruises by the method of Sette and Ahlstrom (1948) for separate spawning areas in Georges Bank and Nantucket Shoals for the months of October-December in 1972 and 1973.

Growth of individual cohorts was determined by the deviation from average frequency method. The deviations were plotted and lines fitted to several of the homologous modes in the manner of Sette (1943) and Saville (1956) with the slopes of the lines estimating growth coefficients. The coefficients for Georges Bank ranged from 0.0034 to 0.0093 with a mean of 0.0063. The average rate of growth slowed as the seasons progressed, with an early value of 0.0075, a midseason value of 0.0060, and a late autumn value of 0.0034. Coefficients for the Nantucket Shoals larvae followed closely those for Georges Bank. Early to late seasonal values of 0.0086, 0.0060, and 0.0032 were estimated with a mean of 0.0059 and a range of 0.0025 to 0.0108. These rates were approximately half of the average seasonal value (0.0165) estimated previously in this study. Growth may have been slower in 1972 and 1973, or the low values may simply be a reflection of the subjectivity used in selecting homologous length modes between cruises.

In order to estimate mortality of specific cohorts within the two sub-areas, the mean ages of larvae from the initial cruise were first determined from the computer program developed under the Sette and Ahlstrom method previously described, the time between the middates of the first and second cruise was added to the mean ages, and the new lengths of the cohort extrapolated. The mortality coefficient ( $Z$ ) and percentage mortality per day was computed between cruises. Not surprisingly, because of the similarity of methods, the cohort mortality rates generally fell within 3-5% per day, similar to the range of values estimated for the average seasonal picture.

## 5. COMPARISON OF POTENTIAL EGG PRODUCTION FROM LARVAL AND VPA ASSESSMENT DATA

Another important calculation from the larval herring surveys is estimation of the 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-production 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-bed mortality between years or areas. To make these computations, information must be available on the relative age composition of the mature stock size, sex ratio, relative fecundity, and egg mortality.

### 5.1 Methods

Sea herring in the Georges Bank - Gulf of Maine area generally become 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 on Georges Bank for the 1960-65 year classes. In recent years, 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 (Anthony and Waring in press). Maturity-at-age data (unpublished) from 1967 to 1976 for the Georges Bank area (ICNAF Statistical Area 5Ze), provided by the Institut für Meereskunde Abt. Fischereibiologie, Federal Republic of Germany, indicated that the proportion of individuals maturing at age 3 was especially high in 1973, perhaps greater than 80%, and in 1971 60% of the population may have been mature at age 3. In all other years since 1967, the proportion of individuals maturing at age 3 appeared to be considerably lower. Estimates of the mature female fraction used in this study were based primarily on the geometric mean of the fraction

mature at age from Boyar's (1968) data. Maturity values of 0.20, 0.91, and 1.00 were used for age classes 3, 4, and 5+, respectively, for all years, except that an additional computation was made for 1973, using a mature fraction of 0.60 at age 3. The VPA stock-size composition was obtained from the Northeast Fisheries Center's most recent estimates of the Georges Bank stock. Sex ratios are approximately 1:1 throughout the Georges Bank and Gulf of Maine area (Scattergood 1952; McKenzie 1964; Pankratov and Sigajev 1973; Giedz 1979). Age-specific fecundity estimates for the Georges Bank area were based on data from Perkins and Anthony (1969) collected in 1963 and 1964. Fecundity (eggs per female) increases exponentially with weight and age of fish.

To estimate the initial production of eggs back-calculated from the larval data, some assumption had to be made about egg mortality, hatching success, and initial larval mortality prior to the time they were vulnerable to plankton nets. Herring spawn in the Georges Bank area on gravelly substrate at a mean depth of 40 m in an environment characterized by strong mixing processes (Drapeau 1973). Along the nearshore area, red algae provide a substrate in waters less than 40 m (McKenzie 1964; Cooper, Uzmann, Clifford, and Pecci 1975). Although eggs may be deposited in layers up to 5-cm thick, observations 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 algae-covered substrate, than in multilayered beds. 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 at a temperature of 10°C (Cooper et al. 1975), 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, 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, a conservative egg-mortality correction factor of 10% was used in this study to estimate potential egg abundance back-calculated from the larval data. Newly hatched yolk sac 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 on the larval herring surveys only sampled to within 5 m of the bottom. No direct observations of larval mortality have been made during the first few days after hatching.

The estimated egg production derived from the larval data was calculated for each season, 1968-77, by first applying an assumed egg-mortality correction factor of 10% to the estimated initial production of larvae (duration and mortality corrected) derived by the two methods of Sette and Ahlstrom (1948) and Saville (1956). Potential egg production derived from the VPA stock assessments was based on age-class composition and age-specific maturity and fecundity data. The number of eggs contributed from the estimated number of mature females within an age class multiplied by its fecundity estimate were summed for the various age classes for a given spawning season. The two egg-production estimates and their ratios are compared in Table 9 for the 1968-77 seasons.

## 5.2 Results

The abundance of recently hatched larvae in the Georges Bank - Nantucket Shoals area is compared with the VPA estimated spawning stock size for the years 1968-77 in Figure 3. The larval abundance curves approximate the form of the VPA spawning stock curve for the 1972-77 period more closely if it is assumed that a high proportion (60% vs 20%) of the 1970 year class reached maturity at age 3 in 1973.

Larval abundance estimates for the 1968-70 seasons are believed to be seriously underestimated because the seasonal total for each year was based upon a single survey, the sampling coverage was inadequate, and because of the sampling gear and towing profiles used. The standard ICNAF larval herring program began in 1971; however, the towing profiles used also lead us to believe that larval abundance may have been underestimated but not to the extent as in 1968-70. The revised ICNAF towing profile initiated in 1972 has

been the standard protocol through the 1977 season. Our data indicate that the 1976 season's initial larval abundance estimates may be underestimated somewhat but the correct value is certainly not as high as that for the 1977 season. There also is the possibility that the VPA estimates of adults were too high, based on a number of special trawl surveys (Waring, Sissenwine, and Dornheim 1979), which would bring the larval and VPA estimates more in line for these years. For these reasons, the 1972-75 seasons represent our best data set of both larval and VPA estimates, and a valid comparison between the two can be made only for these years. In Table 9 the VPA estimate of eggs produced is always larger than the larval estimate and the ratios are very large except for the 1972-75 seasons. The ratios based on the Sette and Ahlstrom method are smaller (within a factor of 4) than those based upon the Saville method (within a factor of 12) for the 1972-75 seasons. The Sette and Ahlstrom method provides our best estimate of larval abundance, and in 1973 our best estimate of the mature female spawning stock is the value derived using a mature fraction of 0.60 at age 3. Therefore, the VPA/larval ratios of eggs produced in 1972 of 1.2 and in 1974 of 1.6 are remarkably close. In both of these years spawning occurred predominantly on Georges Bank. In 1972 and 1975 the ratios are consistently higher, 3.6 and 3.8, respectively, and in both of these years spawning was predominantly on Nantucket Shoals. These higher ratios can possibly be attributed to the fact that our sampling does not cover the shoaler parts of Nantucket Shoals where significant spawning can occur, thereby underestimating the initial abundance of larvae. This also would explain in part why the 1977 season's ratio was so high, as virtually all the spawning occurred on Nantucket Shoals that year, and, as mentioned previously, the VPA stock-size estimates are believed to have been overestimated for 1977. One would expect to get positive VPA/larval egg-abundance ratios assuming significant egg mortality and no other errors in back-calculations of egg production. However, there are two other potential sources of error which could generate significant underestimates of egg production from larval back-calculations, namely (1) higher mortality of recently hatched larvae which are not sampled, and (2) a convex larval growth curve. The fact that the VPA/larval ratios are not larger than they are suggests that these sources of bias may not be particularly large.

## 6. RELATIONSHIP OF LARVAL ABUNDANCE, GROWTH, AND MORTALITY WITH RECRUITMENT

A comparison of the Georges Bank - Nantucket Shoals initial production of larvae from the autumn 1971-77 seasons with abundance of larvae in December shows that the relative abundance of larvae as late as December is still proportional to the initial production estimates. Studies off the Maine coast by Graham et al. (1972) and Graham and Davis (1971) indicated that the initial abundance of larvae in the autumn was reduced to a common level by early winter each year. Although mortality was higher in the autumn than the winter, the winter period was considered critical in that years of low winter mortality were subsequently related to a greater percentage of that year class as 2-year-olds in the juvenile herring fishery. A comparison is made in Table 10 of the relative abundance of the recruited year class as 3-year-olds in the adult herring fishery with larval abundance in February and overwinter (December-February) instantaneous growth and mortality rates for the 1973-77 year classes. Estimating the size of the recruiting year classes has been shown to be inadequate based on research-vessel survey data. Only a relative index of abundance at age 3 of "poor-average-good" is shown in Table 10 and these quality indices are made in comparison to the base period of 1965-73 for the entire region from Cape Hatteras to southwest Nova Scotia. The NEFC's assessment group has recently attempted to use a holistic approach in their VPA stock assessments to overcome other limitations of the unknown amounts of intermixing of herring populations throughout the area, and various fishing mortality (F) rates assumed. The fishery on eastern Georges Bank collapsed in 1976 so that data are just not available for this area. Therefore, catch data have been pooled for all herring fisheries between Cape Hatteras and Nova Scotia for the 1965-77 period. VPA estimates have been applied to the pooled data using various high or low assumed fishing mortality rates to derive a probabilistic assessment of the fishery. The range of the various assessments of age 3's for the 1974-76 period was compared to the base period of 1965-73 to estimate their relative quality index of population size at recruitment. Fluctuations in abundance between the various stocks in the Gulf of Maine generally correspond from year to year.

Initial production of larvae during autumn 1973, from the strong 1970 year class, was the highest recorded in the time series, yet the relative abundance as age-3 recruits was only poor to average. The 1974 and 1975 year classes at age 3 were considered poor and the initial production of larvae was relatively high in 1974 and intermediate in 1975. The predicted "good" recruitment for the 1976 year class comes from a year when larval production on Georges Bank and Nantucket Shoals was the lowest recorded! But so far there is no evidence of recruitment on Georges; instead, it appears that only inshore areas are seeing this recruitment! There does not appear to be any significant relationship between February larval abundance, overwinter growth and mortality rates, and relative abundance as recruits. In fact there is a slight inverse relationship between February larval abundance and recruitment abundance, but the range of larval abundance estimates is not great.

One might expect an inverse relationship between larval growth and mortality; i.e., when growth is high, mortality is low, and the converse. However, this relationship is not clear in all cases. It is difficult to estimate a true population growth rate from the field data as it may be masked by differential size-specific mortality, and the fact that larvae may be on different parts of the growth curve. One might expect that the 1975-77 year classes with low overwinter mortality (<1%/day) would have better recruitment than the 1973 and 1974 year classes when mortality during the same period was 4-5%/day. The 1975 year class had virtually zero winter mortality and one of the highest rates of growth. 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 (Waring 1979). He also reports large numbers of juvenile herring occurring for the first time in a decade in the estuaries of southern Massachusetts by the State Fisheries surveys, summer 1978. The larvae found in Buzzards Bay in 1978 were believed to come from the 1977 year class.

The absolute size of the larvae as they became older may be the important determinant to consider in relation to recruitment success. Referring to Table 8, the mean length of larvae in February of 1976, 1977, and 1978 was significantly greater than in February 1974 and 1975. The mean length of larvae in February 1976 (1975 year class) was about 4 mm greater than the mean length of larvae in February 1975 (1974 year class), and the 1975 year class also was larger in December but the difference was smaller. The greater mean size of larvae from the 1975 year class, compared with the 1974 year class, appeared to be carried through the following late winter and spring cruises of 1975 and 1976, based on individual cruise length frequencies reported by Joakimsson (1976) for March 1975 and 1976, Davis (1975) for May 1975, Davis and Morris (1976) for May 1976, and Grimm (1977) for April 1976. Most of the larval production for the 1974 year class originated on Georges Bank (-84%), whereas larval production for the 1975 year class mostly (-69%) occurred on Nantucket Shoals where more of the population may have recruited to the coastal fishery. By the criteria of relatively low overwinter mortality and large size attainment by February, the 1977 year class also should have good recruitment at age 3. Initiation of spawning has generally been later in these recent years of larger larvae, at the same time a shift appears in spawning location from Georges Bank to Nantucket Shoals. Perhaps survival is better in nearshore waters.

## 7. DISPERSAL OF LARVAE IN RELATION TO EKMAN TRANSPORT

### 7.1 Methods

Fraser (1958) and Saville (1965) emphasize the importance of larval dispersal on recruitment, especially where spawning stocks occupy relatively isolated banks surrounded by deep oceanic water. Small changes in current patterns can cause extreme fluctuations 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). Bumpus (1976) provides a recent review of the physical oceanography of Georges Bank. 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. Dispersal of young herring larvae through the autumn is generally southwesterly at the rate of 1-8 miles per day. However, older larvae are still collected on Georges Bank through the winter and spring. Surface circulation during the winter may respond more to the high, short-term wind effects than during the spring and summer seasons when a clockwise eddy appears to develop. It is generally believed that winds exert their greatest influence on the shallow Georges Bank waters through vertical mixing of the water column. The 10-year mean monthly Ekman transport vectors computed for the Georges Bank area are typically southwest from September through March, reaching maximum magnitude in January; but significant variations occur within months and seasons (provided by the Atlantic Environmental Group, NMFS, Narragansett, Rhode Island).

In this section we examine the dispersal of larvae from the Georges Bank and Nantucket Shoals spawning sites in relation to weekly estimates of Ekman transport. The main larval concentrations for most cruises were designated by stations with densities greater than 10 larvae per 10m<sup>2</sup> for a given size group. On cruises where numbers of larvae were very low, the main larval concentrations were marked with lower densities: for the February 1974 and 1975 surveys, concentrations were defined as densities greater than 5 larvae per 10m<sup>2</sup>; and for all the 1976 and 1977 surveys, greater than 1 per 10m<sup>2</sup>. Based on the fact that herring larvae grow approximately 5 mm per month, and that the surveys were conducted approximately at monthly intervals, larvae less than 10 mm in length were considered recently hatched and represent the general spawning areas. Larvae from each succeeding 5-mm length class from successive cruises were plotted on one chart in order to follow the dispersal of larvae from an individual spawning population through the season. The best example of larval dispersal was chosen for each of the 1971-77 seasons (pictured in Figures 4-10). The arrows in the figures represent the inferred spread of larger larvae from the spawning areas.

On the same figures illustrating the seasonal larval dispersal of a given length group, weekly Ekman transport vectors are shown in relation to the survey midpoints. The transport data were produced by the Pacific Environmental Group of NMFS for the northeast Georges Bank area (42°N, 66°W) and made available by the Atlantic Environmental Group. Each weekly mean was computed from 28 6-hourly synoptic samplings based on atmospheric pressure charts by the method of Bakun (1973). Examination of the Ekman transport vectors also provided for the Nantucket Shoals area (42°N, 69°W) indicated that values for the two areas represent each other fairly well.

Bumpus (1976) made some preliminary summaries of larval herring dispersal in a similar manner, looking only at the first three length classes, comparing their spread between successive cruises for the 1972-74 seasons with *monthly* Ekman transport estimates. Weekly transport values have been used here 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, Boicourt, and Hansen 1978). Bumpus (1976) states that in the shallow waters of Georges Bank and Nantucket Shoals water movement may be more directed downwind, i.e., 90° to the left of the Ekman transport vectors shown in Figures 4-10. He also observed that the position of the fronts near the edge of the Bank in the last half of 1973 and all of 1974 did not correlate well with the monthly Ekman transport vectors and indicates that the development of eddies north of the Gulf Stream may possibly have a significant impact on the location of the Shelf Water - Slope Water front. Anticyclonic eddies occurred near the southern edge of Georges Bank in autumn 1972, 1974, February-April 1976, and throughout the year in 1977 (Bisagni 1976; Chamberlin 1978; Mizenko and Chamberlin in press a,b).

## 7.2 Results

1971 Season (Figure 4). By the second cruise the main spawning population in the northeast part of Georges Bank had begun to disperse in a southerly direction. Between the second and third cruises, advection was to the south and west along the southern edge of Georges. Between the third and fourth cruises, three separate patches of larvae were located across Georges Bank in a north, central, and southern position. Their latitudinal orientation and westward drift corresponds with the strong northwesterly computed Ekman transport for the period 17-24 October. By the fifth cruise, westward advection of

larvae extended across the central part of Georges, apparently a coalescing of the two patches of 15-20-mm larvae from the previous cruise. Ekman transport values for the period between the fourth and fifth cruises indicated an extremely strong westward component.

1972 Season (Figure 5). Larvae originating from the Georges Bank spawning area were rapidly advected to the north, south, and west by the second cruise. Between the second and third cruises, the 15-20-mm larvae continued to disperse northwest and southwest beyond the 100-m contour. During the period between the third and fourth cruises, an extremely strong northwest Ekman transport was computed, probably transporting a significant part of the larval population off the northern edge of Georges as only a small group of 20-25-mm larvae remained on the central part of the Bank by the fourth cruise.

1973 Season (Figure 6). Production of larvae in 1973 was the highest recorded of the time series so that by the second cruise larvae from the first cruise spawning area had spread to the southwest covering most of the northeast part of Georges within the 100-m contour. Between the second and third cruises, larvae were advected off the northeast peak of Georges and to the southwest along the northern and southern edge of Georges. Larvae originating in Nantucket Shoals had an easterly and southerly drift, as well as a northeasterly turn across the northern part of the Great South Channel. By the fourth cruise, larvae had expanded eastward from Nantucket Shoals and significant blobs of larvae were found beyond the 100-m contour along the southern and northeastern edge of the Bank. Strong southeasterly Ekman transport values persisted throughout the latter part of October-November. A significant portion of the larval population may have been transported off the Bank between the fourth and fifth cruises since by the latter cruise the 20-25-mm larvae were restricted to a relatively small area mostly within the 100-m contour.

1974 Season (Figure 7). Larvae from the first-cruise spawning area were spread across the northeastern peak of Georges Bank with a distinct tongue of larvae advecting off the peak to the southeast. On Nantucket Shoals, larvae from the initial spawning area were spreading along a northwest-southeast axis with a slight eastward spread across the Channel. Between the first and second cruises there was a marked advection of larvae from both spawning areas to the southwest. Larvae from the northeastern part of Georges advected along both the northern and southern edges extending beyond the 100-m contour. Significant transport beyond Georges Bank seemed to have occurred across the northwestern edge into the Gulf of Maine. Between the second and third cruises, larvae covered the entire Georges Bank - Nantucket Shoals area within the 100-m contour. Ekman transport values show an extremely strong advection to the northwest during this period, but the larval population originating from northeastern Georges appears to have been transported in a westerly direction across the banks, directly downwind. Larvae off the northwestern part of Georges by the second cruise may have been pushed back on the shoals by the third cruise. By the fourth cruise the distribution of the 20-25-mm larvae was reduced to smaller areas within the 100-m contour.

1975 Season (Figure 8). A large intrusion of shelf water onto Georges Bank occurred in September-October of 1975 (Gunn 1978), which may have been associated with the increased Gulf Stream eddy activity reported by Chamberlin (1978). Three spawning areas were in evidence by the second cruise: one on the northeast part of Georges Bank, another on the northwestern edge of Georges, and a third on Nantucket Shoals. By the third cruise, larvae from the northeastern Georges spawning area were being advected to the southwest and lobes of larvae were coming off the peak. Larvae originating from the northwestern edge of Georges and the Nantucket Shoals area were being advected north into the Gulf of Maine and south across the banks. A strong southwest advection occurred for the Nantucket Shoals larvae. There is also some evidence of a general eastward spread of larvae from the Nantucket Shoals spawning area across the Great South Channel and from Georges Bank spawning areas eastward along the northern edge. Between the third and fourth cruises, the main larval population was residing in the Gulf of Maine north of the Great South Channel and along the northern part of the Bank. Ekman values show two alternate weeks of very strong northwesterly transport during this same period. Between the fourth and fifth cruises, larvae were present in

only three centrally located areas on Georges Bank - Nantucket Shoals. During this same period, Ekman transport was predominantly to the southwest and southeast. February 1976 had a particularly strong southwest Ekman transport which may have pushed larvae back onto the banks from its more northerly position in December 1975.

1976 Season (Figure 9). Production of larvae during the 1976 season was extremely low. Total numbers of larvae for all sizes are delineated for each cruise in Figure 9. A clear picture of dispersal for this season was not possible because of the scarcity of data; however, some general distributional patterns can be observed. Some spawning activity had occurred on the northeastern and northwestern parts of Georges Bank, as by the first cruise young larvae were collected in these areas. Larvae originating from historical spawning beds on northeast Georges had already advected south along the edge of the Bank. Ekman values indicated strong transport to the southeast during all of October. By the second and third cruises, young larvae were still being produced across northern Georges with some indication of smaller amounts in the Nantucket Shoals. Extremely strong south-southeasterly transport was computed for late fall and winter. The winter of 1976-77 has been reported by Ingham (in press) to have produced unusually strong, persistent northwesterly winds in the Georges Bank and Middle Atlantic Bight area in January and February which produced strong southwestward Ekman transports in the upper layers of the sea. By the fourth cruise in February 1977, larvae were found in very low densities scattered across the shoals from northern Georges to Southern New England. A large number of anticyclonic eddies were produced in winter-spring of 1977 compared to the previous 3 years (Mizenko and Chamberlin in press b).

1977 Season (Figure 10). The 1977 season's larval production also was very low. Most of the spawning occurred in the Nantucket Shoals with smaller amounts across the northern edge of Georges Bank. Larval areas were grouped by 10-mm length classes because of low densities in order to depict any pattern. Between the first and second cruises there was a northerly spread of larvae into the Gulf of Maine from the northern edge of the banks. Larvae south of the northern edge tended to move in a southerly direction. A tongue of larvae from the southern part of the Nantucket Shoals spawning area advected in a southwesterly direction. Ekman transport values show a strong northerly component during this period; however, a large eddy was located along the southern edge of the banks which may have been entraining water off the banks at the same time. By the third cruise the distribution of larvae was restricted more to the shoals area. Two tongues of larvae originating from the Nantucket Shoals spawning area encircled Cape Cod by this time. Strong southerly transport values were computed for this period. Only a few small patches of larvae were present on the shoals by the fourth cruise.

## 8. SYNTHESIS AND SUMMARY

The major objective of the ICNAF larval herring surveys was to provide a time series of larval production estimates derived from a fairly discrete spawning stock, of sufficient scope and intensity in both geographic extent and temporal coverage during each spawning season to gain insight into the major biotic and abiotic factors that control larval survival during the first 6 months of life; and then to try to relate the various conditions associated with each larval brood to the subsequent recruitment of the year class. Significant variations in larval abundance, mortality, growth, and dispersal were observed over the 1971-77 seasons for the Georges Bank - Nantucket Shoals spawning stock. The interrelationships between larval survival, spawning stock, environmental factors, and recruitment are examined here for a better understanding of their dynamics.

Differential mortality during the larval period is generally regarded as the major cause of year-class fluctuations. Recruitment success has been viewed in terms of the critical-period concept (see May 1974 for a recent review), i.e., there is a brief period of high larval mortality, and survival

through this period leads to variations in the size of the year class. Hjort (1914) proposed that high mortality may take place at the end of yolk sac resorption. Subsequent larval fish studies attempting to define the shape of the survival curve have not completely validated the critical-period concept. It is conceivable that there may be more than one period of high mortality, particularly for herring, where the length of larval life for herring spawning in the autumn and reaching metamorphosis in the spring is considerably longer than the month or two typical of most other marine larval fish. Dragesund and Nakken (1971) found a 94% mortality of Norwegian spring herring larvae by the end of yolk sac resorption, corresponding to an instantaneous daily mortality of 27%. Saville (1965) reports a marked reduction of spring Clyde herring larvae shortly after the main hatching peak with apparent mortality rates of 35% and 18% per day in 2 years. Also, Graham and Chenoweth (1973) estimated a 75% mortality (29% per day) of Georges Bank larvae less than 10 mm in length over 4 days in October 1970. Their average instantaneous mortality rate of 28% per day for recently hatched larvae is considerably higher than the average September-February rate of 4% per day found in this study. The seasonal average mortality rate of 3-5% per day found for the Georges Bank - Nantucket Shoals larvae is similar to the rates found by Graham and Davis (1971) for western Gulf of Maine herring larvae and by Wood and Burd (1976) for herring larvae in the central North Sea. There is, so far with the 0.505-mm mesh data, no evidence in our analysis of the Georges Bank - Nantucket Shoals larval herring data to indicate an initial period of high mortality. Looking *only* at the 1972-75 data (years for which *both* larval production and VPA estimates are thought to be reasonably accurate--at least free from major biases or errors) we noted that the consistent pattern of lower egg-production estimates derived from larval data (relative to VPA) may be due in part to higher mortality at earlier stages. However, the relative differences in the egg-production estimates derived from the VPA and larval data are smallest for the 2 years of high larval production, i.e., 1973 and 1974, suggesting that early mortality was lower rather than higher during the higher larval densities. That is, if post-hatching mortality in the first few weeks was directly related to density of larvae and it was substantially higher than mortality of older larvae, then one would expect that back-calculated estimates of egg production derived as for Georges Bank would have a higher negative bias relative to VPA estimates in years of higher larval production. Just the reverse is true for the Georges Bank data for the years 1972-75; thus these data are not consistent with the notion that severe density-dependent mortality occurred in early larval stages. In any case, an initial period of high mortality need *not* have any particular significance for year-class success unless it was massive.

A comparison of the initial larval herring production estimates over the 1971-77 season (Table 6) with their average seasonal mortality (Table 5) might suggest a density-dependent relationship. Average mortality of larger larvae, 10-20 mm, September-December, was higher during years of high larval production; however, the 1975 season with intermediate production had the highest estimated larval mortality through December, and the 1973 season with the highest larval production had a September-December mortality rate which was intermediate between the 1972 and 1974 seasons (Table 5). But, if the winter period is added to the 1975 season, the high survival of larvae between December and February compensates for the high initial autumn mortality, lowering it to 2.74% per day. There were no February cruises for the 1972 and 1971 seasons to compare overwinter mortality with the autumn estimates. The implication here is that there are at least three periods or stages of herring larvae that should be treated separately: (1) recently hatched larvae less than 10 mm, (2) larger larvae of about 10-20 mm during the autumn, and (3) larvae greater than 20 mm during the overwinter period. Survival rates and causes of mortality may be quite different during each of these periods which could be masked by average seasonal mortality rates.

There is some evidence from this study and that of Graham, Chenoweth, and Davis (1972) that variations in larval herring survival over the winter period is related to subsequent year-class size. Winter instantaneous mortality rates ranged from "0" to 5% per day for Georges Bank - Nantucket Shoals larvae during 5 overwinter periods in this study. Mortality tended to be higher through the winter when larval abundance was high in December, but a clear inverse relationship was not evident. Also, an inverse relationship between mortality and growth was not readily apparent. However, there was an indication that larger mean size of larvae by February may be related to good recruitment. The larger mean size of larvae in December, and particularly the

increased growth during the overwinter period since 1975, has been observed in recent years when spawning was delayed until late October and there was a shift in spawning location from Georges Bank to Nantucket Shoals. If anything, we would expect the population of larvae spawned later in the season in recent years to be smaller by December, compared to larvae spawned earlier in the season in former years. For the year classes 1975-77, a very low (<1%) overwinter mortality was observed when the population mean size was >30-mm length in February. It would be interesting to see if these same groups of larvae of greater mean size in the overwinter time series also were of greater size in the autumn beginning as recently hatched larvae. But the intermixing of the multiple spawning cohorts in the autumn presents a precise estimation of individual cohort mean size and growth through this period.

Cushing (1972) proposed three mechanisms governing recruitment in marine fishes: (1) density-independent or environmental factors, (2) density-dependent factors, and (3) competition; all 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 (1974), Cushing (1973, 1974, 1975), Cushing and Harris (1973), and Ware (1975) emphasize the link between larval growth and mortality as density-dependent processes regulated by the availability of food. The degree to which larvae are able to grow quickly through a succession of decreasing predatory fields, thereby reducing mortality, determines their potential population size. The major cause of larval mortality is believed to be predation, which may become increasingly important at low food levels where larvae may be on the verge of starvation, but is of lesser importance as a density-dependent process at high food levels.

Sherman and Honey (1971) and Chenoweth (1970) observed that feeding incidence and condition of larval herring were low during the winter when plankton volumes were low along the coastal Gulf of Maine. The seasonal variation in the food of larval herring in coastal waters of Maine has been described by Sherman and Honey (1971) and Sherman, Honey, Sullivan, and Busch (1976). Major food organisms of larval herring reflect the dominant species of copepods in the area. Prey selection and condition of herring larvae in relation to changes in zooplankton populations on Georges Bank - Nantucket Shoals for a number of selected seasons is being undertaken at NEFC. Preliminary results indicate that the very low mortality rate and greater mean size of larvae during the 1975-76 winter, compared to 1974-75, was coincident with a greater percentage feeding and some suggestion of an increase in their principal food organisms. 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 zooplankton species. Wind mixing of Georges Bank waters also was very strong during the 1976-77 winter (Wright 1978) when larval mortality was low.

A general warming trend of 2-3°C during the autumn has been observed by Davis (1978) for Georges Bank bottom temperatures, particularly since 1971, peaking in 1973, 1974, and 1976, 1977. Zooplankton biomass on Georges Bank followed the temperature trend, increasing from moderate levels in autumn of 1971 and 1972 to a high in 1973, declining in 1974 to a low in 1975, and high again in 1977 (Sherman, Sullivan, and Byron 1978). The plankton biomass data for autumn 1976 are not yet available. It is interesting to note that the high 1975 autumn larval herring mortality occurred during the low plankton biomass, which may reflect lower food availability, followed by the high 1975-76 overwinter survival when there was believed to be an increase in their principal food organisms. Davis (1978) reported the highest adjusted mean temperature in a decade for Georges Bank during the autumn of 1976 and 1977. If there is a correlation between warm autumn water temperature and high zooplankton biomass, then the 1976 autumn also should have a high biomass. The good predicted recruitment for the 1976 year class may be related to the high zooplankton biomass if it represents increased food availability for the larvae. Water temperature and zooplankton biomass were high in autumn 1977 when larval mortality was relatively low during the autumn and extremely low during the overwinter period. Larval mean size by December 1977 and February 1978 was the highest recorded of the time series. Coupled with the fact that unusually large numbers of juvenile herring from the 1977 year class have been observed for the first time in many years in the estuaries along southern Massachusetts, the 1977 year class may prove to be a strong one.

We have attempted to construct a temperature history of the Georges Bank and Nantucket Shoals larval populations by size class through each of the 1971-77 seasons for comparison. In general, their temperature history followed the water-temperature trends for the subarea. However, since we do not have very precise growth estimates from the field data, seasonal comparisons are of limited value.

In order to satisfactorily address the question of competition of fish larvae for the available food organisms, one needs to know the minimum range of suitable prey organisms for a larva of a given size to survive in relation to all other members of the zooplankton community feeding on the same potential prey. Zooplankton data from the larval herring time series are not available yet but the ichthyoplankton has been summarized for a number of years. Wyatt (1974) has provided some evidence of a possible competitive situation between plaice and sand eel larvae feeding on *Oikopleura dioica*. The dominant ichthyoplankton from the 1974-76 seasons' larval herring surveys are ranked in Table 11 for the separate areas of Georges Bank and Nantucket Shoals within the 100-m depth contour. The hake larvae were dominant in early autumn, herring larvae from mid-autumn to early winter, and cod, pollock, haddock, and sand lance larvae from winter through spring. The three or four 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 three years, important differences in their relative ranking and geographical 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 1974-77 winters between Cape Hatteras and Georges Bank was documented by Smith, Sullivan, and Berrien (1978). During 1976-77 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 noted. Peaks of larval abundance are generally successional and their 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 between them. Our preliminary larval gut analyses of both species support this view. It does not appear, therefore, that any direct competition between larval fish is limited.

The role of predation on larval fish populations is difficult to ascertain as there is very little quantitative information available. Many species of plankton and fish are known to prey upon fish larvae (Lebour 1922, 1923; Pearcy 1962; Fraser 1969; Lillelund and Lasker 1974; Theilacker and Lasker 1974; Daan 1976; von Westerhagen and Rosenthal 1976; Harding, Nichols, and Tungate 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 Gulf of Maine waters, were observed throughout the Georges Bank during the autumn and winter of 1975-76 (Rogers, Biggs, and Cooper 1978). Recall that larval herring mortality in September-December 1975 was the highest observed (Table 5); however, the December-February 1976 mortality was the lowest observed (Table 7). Dense concentrations of the chaetognath, *Sagitta elegans*, also are found on Georges Bank and Nantucket Shoals (Redfield and Beale 1940; Clark, Pierce, and Bumpus 1943) and could possibly account for heavy predation on small fish larvae (Kuhlmann 1977). However, chaetognaths may play a more important role as potential competitors for the same copepod prey, or they may in some way disrupt normal feeding behavior of larvae.

The dispersal of herring larvae during the 1971-77 seasons will form a basis for further comparison here with what we know about the effect of environmental conditions on survival, suitable planktonic prey as food organisms, and possible competitors and predators. In this study we found a general correspondence in the direction and magnitude of larval dispersal from their spawning areas with the weekly computed Ekman transport, especially during periods of unusually high transport. Anticyclonic warm-water eddies moving near the southern edge of the Bank also are believed to play an important role in the movement of shelf/slope waters, both on and off the banks. Transport of herring larvae across the 100-m depth contour occurred frequently through the time series, both south across the shelf/slope-water front and

north into the Gulf of Maine, but their loss appeared to be small relative to the total population. Some portion of the larval population always remained within the central part of the banks through the winter and spring. Short-term wind stress, even if severe, may affect only the upper few meters of the water column. Early herring larvae are spread throughout the water column, centered around the mean depth to bottom (Lough unpublished data). Therefore, the short-term effects of wind may be small relative to transport by the long-term residual or shelf/slope interactions. Warm-core eddies moving south of Georges may entrain a significantly greater volume of water off the banks, affecting larvae deeper in the water column. Perhaps advective processes play a more important role during the first couple of months of larval life when larvae are small, but as they grow larger their increased ability to perform vertical migrations in the water column (see Seliverstov 1974 for review) may aid them in maintaining their position on the banks. Strong, semidiurnal rotary tidal currents with speeds greater than 2 knots and ellipses 4-8 miles in length are a distinctive feature of Georges Bank and may be an important retention mechanism for many endemic plankton species.

The autumn 1971 mean monthly transport values were most typical of the long-term average condition compared to more recent years. There also appeared to be a high degree of larval herring retention on Georges Bank through the 1971 autumn, which corresponds with the lowest autumn average mortality rate of 3.2% per day for the time series (excluding the 1976 autumn for which we do not have a reliable estimate). The higher autumn larval mortalities (4-5% per day) for the 1972-74 seasons occurred when larval production was high and larval populations moved closer to the southern edge of the Bank. Advection of larvae across the southern edge of the Bank was quite evident during the 1973 season, corresponding with the strong southerly Ekman transport in late October-November. The 1975 season represents a special case in which the autumn mortality of 5.2% per day, the highest mortality of the time series, was followed by essentially "0" mortality through the winter. By December most of the larval population from spawning beds on Nantucket Shoals and Georges Bank had drifted into the Gulf of Maine north of the Great South Channel; but by February it appeared to have moved back onto the central part of the banks. The computed Ekman transport estimates tended to corroborate this movement. High larval mortality may have occurred due to their transport off the Bank during late autumn in 1975. Production of larvae was very low for the 1976 season at a time when strong southerly transport was estimated; however, larvae spawned on Georges Bank were still there through the winter and spring. The distributional pattern of larvae for the 1977 season was similar to that in 1975 when larvae were transported into the Gulf of Maine. Both of these autumns were characterized by generally weak transport values. However, the average autumn mortality rate of 3.2% per day in 1977 was lower than that in 1975 (5.2%). Nearly all the 1977 season's production occurred in the Nantucket Shoals and it is probable that survival may be better near shore than on Georges Bank. As mentioned previously, the mortality rate would be underestimated for larvae spawning in the Nantucket Shoals where we cannot adequately sample them inshore.

There does not appear to be any single critical period in larval herring survival which determines year-class size. Instead there may be several periods such as envisioned by Gulland (1964) where differential mortality may have important effects such as survival of the very young larvae in the autumn and/or larger larvae through the winter period, or it may be a continuous process. What we observe during the overwinter period is greater expression of differential survival when it becomes most apparent in late larval life. From the limited information available in the time series, the attainment of a relatively large size of the larvae by winter appears to be related to good recruitment. This hypothesis states that fast growth, resulting in a larger size, is conducive to good survival for a number of reasons, one being that larvae are able to escape through a succession of decreasing predatory fields. Larger larvae appear to have better survival through the winter period when food may be limited. An increasingly larger mean size of larvae during winter was observed in this study, particularly in recent years; however, the larger size of these larvae appears to have been established early in larval life during the previous autumn. 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). The same situation may apply to herring in the Georges Bank region. Maturing adult females feeding during periods of increased productivity may be able to provide their offspring with a survival advantage by producing more robust eggs and larvae,

providing a direct link between the carrying capacity of the environment and future stock size. This initial advantage can be modified by conditions during the larval period to provide additional feedback between potential population size and environmental limits. While starvation-predation may be the major cause of larval mortality, we need to view this in terms of population dispersal in relation to changing current patterns. Intimate knowledge of the hydrography and zooplankton communities of the region is needed to assess the availability of food organisms. Also, more knowledge is required to assess the impact of potential predators. Good survival for larval herring populations in the Georges Bank area seems to occur during those seasons when water temperatures are relatively warm, with sufficiently strong mixing of waters which would increase the productivity of the Bank and accelerate larval growth, as well as the establishment of current patterns to retain the early larvae on the banks where conditions seem to be most favorable for their survival. There is so much variation in the way environmental factors can affect larval herring survival that each season almost has to be studied as a unique case history if we are to gain a real understanding of the processes involved. Only through intensive, multidisciplinary "patch"-type studies, carried out on all scales of sampling throughout the entire early life history of a species can we effectively hope to achieve this understanding.

In conclusion, recruitment is not dependent upon spawning stock size over a wide range of stock sizes, but it does appear that the spawning stock on eastern Georges collapsed after 1976, and the effect of continued heavy fishing on a low stock cannot be ruled out here. In fact, the pattern on Georges Bank (collapse of a spawning stock and shift of the later spawning activity to other sites) has been observed in other places, notably the North Sea. 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 is determined to a great extent by a number of complex factors operating throughout the early life history. There appear to be interconnecting links between a population and its environment during all periods of life, and to understand these linking mechanisms we need a more comprehensive and detailed approach to a study of the recruitment process in a manner recently outlined by Lett and Kohler (1976).

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Table 1. Summary of 37 ICNAF larval herring surveys, 1968-1978, conducted in the Georges Bank-Nantucket Shoals area.

Vessel	Cruise number	Country	Dates
		<u>1968 season</u>	
ALBATROSS IV	68-17	USA	28 Oct. - 26 Nov. 1968
		<u>1969 season</u>	
ALBATROSS IV	69-11	USA	27 Oct. - 23 Nov. 1969
		<u>1970 season</u>	
ALBATROSS IV	70-06	USA	15 Oct. - 21 Nov. 1970
		<u>1971 season</u>	
CRYOS	71-01	FRA	09-24 Sept. 1971
DELAWARE II	71-04	USA	21 Sept. - 04 Oct. 1971
VIANDRA	71-01	USSR	09-25 Oct. 1971
WALTHER HERWIG	71-01	FRG	23 Oct. - 12 Nov. 1971
ALBATROSS IV	71-07	USA	02-17 Dec. 1971
		<u>1972 season</u>	
ARGUS	72-01	USSR	22-30 Sept. 1972
WIECZNO	72-01	POL	02-28 Oct. 1972
ARGUS	72-02	USSR	12-28 Oct. 1972
ANTON DOHRN	72-01	FRG	31 Oct.-12 Nov. 1972
ALBATROSS IV	72-09	USA	02-20 Dec. 1972
		<u>1973 season</u>	
CRYOS	73-01	FRA	16-28 Sept. 1973
WIECZNO	73-40	POL	29 Sept.- 20 Oct. 1973
BEOGORSK	73-01	USSR	15 Oct. - 01 Nov. 1973
WALTHER HERWIG	73-43	FRG	28 Oct. - 08 Nov. 1973
ALBATROSS IV	73-09	USA	04-20 Dec. 1973
ALBATROSS IV	74-02	USA	11-22 Feb. 1974
		<u>1974 season</u>	
WIECZNO	74-01	POL	27 Sept. - 18 Oct. 1974
PROGNOZ	74-01	USSR	18-30 Oct. 1974
ANTON DOHRN	74-01	FRG	16-23 Nov. 1974
ALBATROSS IV	74-13	USA	04-19 Dec. 1974
ALBATROSS IV	75-02	USA	12-28 Feb. 1975
		<u>1975 season</u>	
BEOGORSK	75-02	USSR	25 Sept. - 08 Oct. 1975
BEOGORSK	75-03	USSR	17-30 Oct. 1975
ANTON DOHRN	75-187	FRG	01-18 Nov. 1975
ALBATROSS IV	75-14	USA	05-17 Dec. 1975
ALBATROSS IV	76-01	USA	10-25 Feb. 1976
		<u>1976 season</u>	
WIECZNO	76-03	POL	14 Oct. - 03 Nov. 1976
ANTON DOHRN	76-02	FRG	15-29 Nov. 1976
RESEARCHER	76-01	USA	27 Nov. - 11 Dec. 1976
MT. MITCHELL	77-01	USA	13-24 Feb. 1977
		<u>1977 season</u>	
WIECZNO	77-06	POL	04-24 Oct. 1977
ANTON DOHRN	77-03	FRG	09-19 Nov. 1977
DELAWARE II	77-13	USA	08-20 Dec. 1977
ALBATROSS IV	78-02	USA	14-22 Feb. 1978

Table 2. Summary of cruise estimated abundance of herring larvae by length classes for the Georges Bank-Nantucket Shoals area, 1968-77 seasons.

Year	Vessel	Cruise No.	Middate of cruise	Area Surveyed (m <sup>2</sup> x 10 <sup>9</sup> )	Percentage positive area for larvae	Cruise Estimated Abundance (No. Larvae x 10 <sup>-9</sup> )										Total	
						<10	10-15	15-20	20-25	25-30	30-35	35-40	>40				
1968	Albatross IV	68-17	28 Oct.	63.80	54.55	117.70	165.30	139.50	15.60	1.10							439.20
1969	Albatross IV	69-11	01 Nov.	61.48	41.51	12.50	539.50	427.20	32.50	7.20	0.30						1019.20
1970	Albatross IV	70-60	22 Oct.	76.56	51.52	416.90	535.90	51.90	11.00								1015.70
1971	Cryos	71-01	16 Sep.	78.88	17.65	224.23	14.78										239.01
	Delaware II	71-04	27 Sep.	82.36	26.76	395.15	64.34	27.30	0.26	0.06							487.11
	Vandora	71-01	17 Oct.	77.14	60.15	322.21	260.48	155.87	67.45	16.10	0.24						822.35
	Walther Herwig	71-01	05 Nov.	81.20	47.14	99.64	332.25	85.13	31.57	7.29	1.34						557.22
	Albatross IV	71-07	09 Dec.	83.52	55.56	3.11	28.26	214.29	103.59	4.21	0.32						353.78
1972	Argus	72-01	26 Sep.	52.20	17.78	64.35	48.12	2.50	0.12								115.09
	Wieczno	72-01	14 Oct.	92.80	46.25	313.14	394.25	116.58	3.42	0.75							828.14
	Argus	72-02	20 Oct.	87.00	58.67	807.91	322.25	314.41	21.61								1466.18
	Anton Dohrn	72-01	05 Nov.	90.48	66.67	258.61	214.05	57.32	10.29	0.16							540.43
	Albatross IV	72-09	10 Dec.	93.96	61.73	1.01	73.51	80.92	24.08	2.38	0.24						182.14
1973	Cryos	73-01	19 Sep.	51.04	13.64	136.22	5.26										141.48
	Wieczno	73-40	09 Oct.	92.80	42.50	2661.04	600.80	121.82	8.01								3391.67
	Belogorsk	73-01	23 Oct.	93.96	70.37	6557.43	1495.71	808.18	52.27	0.32	0.16						8917.07
	Walther Herwig	73-43	02 Nov.	92.80	77.50	2624.32	779.52	517.92	88.29	10.75							4020.80
	Albatross IV	73-09	13 Dec.	95.12	86.59	105.87	136.09	476.69	269.75	9.60	0.65						998.65
	Albatross IV	74-02	14 Feb.	66.12	54.39	0.40	0.43	7.99	21.90	16.96	2.97						50.65
1974	Wieczno	74-01	07 Oct.	96.28	24.10	1524.46	5.96	0.92									1531.34
	Prognoz	74-01	24 Oct.	91.64	72.15	4635.68	833.94	53.11	1.98								5524.71
	Anton Dohrn	74-01	19 Nov.	81.20	81.43	1196.33	648.14	429.29	41.90	1.24							2316.82
	Albatross IV	74-13	13 Dec.	96.28	74.70	16.37	523.21	454.60	201.42	17.54	0.68						1213.02
	Albatross IV	75-02	14 Feb.	91.64	48.10			1.32	16.30	37.68	14.66	0.96	0.19				71.11
1975	Belogorsk	75-02	01 Oct.	93.96	15.43	65.02	0.47	0.63									66.12
	Belogorsk	75-03	23 Oct.	95.12	60.37	2426.26	529.40	14.19									2969.85
	Anton Dohrn	75-187	09 Nov.	100.92	70.11	497.71	854.27	241.66	2.20								1595.84
	Albatross IV	75-14	09 Dec.	96.28	62.65	7.02	31.91	125.52	42.05	4.06	0.17						210.73
	Albatross IV	76-01	16 Feb.	99.76	45.35			1.95	44.47	85.14	16.13						148.69
1976	Wieczno	76-03	24 Oct.	96.28	15.36	2.39	23.84	5.89	0.12								32.24
	Anton Dohrn	76-02	22 Nov.	96.28	20.48		0.30	3.49	8.01	0.40							12.20
	Resarcher	76-01	04 Dec.	84.68	31.85		0.15	2.49	7.10	1.11							10.85
	Mt. Mitchell	77-01	18 Feb.	95.12	23.48				1.55	3.72	1.77						7.04
1977	Wieczno	77-06	14 Oct.	63.80	21.79	306.48	77.62	5.69	2.56								392.35
	Anton Dohrn	77-03	09 Nov.	93.96	49.38	16.40	111.70	215.53	2.42								346.05
	Delaware II	77-13	14 Dec.	68.44	34.75		7.96	0.90	5.97	2.21							17.04
	Albatross IV	78-02	24 Feb.	96.28	16.87				0.30	1.25	2.13	2.16	0.43				6.27

Table 3. Mean numbers of herring larvae per 10m<sup>2</sup> on Georges Bank, and associated standard deviations and coefficients of variation. For 37 standard ICMAF stations east of and including the transect on 68° west longitude (see Figure 1).

Cruise	1972				1973				1974					
	Size (mm)	$\bar{X}$	SD	SD/ $\bar{X}$	Cruise	Size (mm)	$\bar{X}$	SD	SD/ $\bar{X}$	Cruise	Size (mm)	$\bar{X}$	SD	SD/ $\bar{X}$
ARGUS 22-30 Sep	5-10	15	83	5.5	CRYOS 16-28 Sep	5-10	32	120	3.7	CRYOS 02-24 Sep	5-10	0	-	-
	10-15	11	44	4.0		10-15	1	5	5.0		10-15	0	-	-
ARGUS 12-28 Oct	5-10	3	8	2.7	WIECZNO 29 Sep-20 Oct	5-10	489	1,833	3.7	WIECZNO 27 Sep-18 Oct	5-10	291	1,050	3.6
	10-15	30	60	2.0		10-15	397	1,578	3.9		10-15	0.4	1.5	3.8
WIECZNO 02-28 Oct	5-10	31	131	4.2	BELOGORSK 15 Oct-01 Nov	5-10	671	3,107	4.6	PROGNOZ 18-30 Oct	5-10	1,026	2,403	2.3
	10-15	52	132	2.5		10-15	133	269	2.0		10-15	179	343	1.9
A. DOHRN 31 Oct-12 Nov	5-10	7	22	3.1	M. HERMIG 28 Oct-08 Nov	5-10	387	1,679	4.3	A. DOHRN 16-12 Nov	5-10	93	304	4.1
	10-15	7	16	2.3		10-15	125	300	2.4		10-15	83	143	1.7
AL IV 02-20 Dec	5-10	0	-	-	AL IV 04-20 Dec	5-10	12	61	5.1	AL IV 04-19 Dec	5-10	1.1	4.6	4.2
	10-15	1	4	4.0		10-15	6	14	2.3		10-15	59	168	2.8

Cruise	1975				1976				
	Size (mm)	$\bar{X}$	SD	SD/ $\bar{X}$	Cruise	Size (mm)	$\bar{X}$	SD	SD/ $\bar{X}$
BELOGORSK 25 Sep-08 Oct	5-10	10	40	4.0	WIECZNO 14 Oct-03 Nov	5-10	0.5	1.5	3.0
	10-15	-	-	-		10-15	5	18.7	3.7
BELOGORSK 17-30 Oct	5-10	84	359	4.3	A. DOHRN 15-29 Nov	5-10	0	-	-
	10-15	52	133	2.6		10-15	0	-	-
A. DOHRN 01-18 Nov	5-10	85	267	3.1	RESEARCHER 27 Nov-11 Dec	5-10	0	-	-
	10-15	85	161	1.9		10-15	0	-	-
AL IV 05-17 Dec	5-10	1	8	8					
	10-15	2	4	2					

Table 4. Seasonal hatching dates and initial abundance estimates of herring larvae (<10 mm standard length) for the Georges Bank-Nantucket Shoals area, 1968-77, based on the normal curve approximation method of Saville (1956).

Season	Total days	Dates	Julian m/d/date	Weighted m/d/date	No. cruises	Range	Initial Larval Abundance Estimates ( $\times 10^{11}$ )			
							Arithmetic mean	Standard deviation	Geometric mean	Standard deviation
1968 <sup>1</sup>	107	12 Sept-28 Dec	4 Nov	21 Oct	1	-	59.301	-	-	-
1969 <sup>1</sup>	107	12 Sept-28 Dec	4 Nov	21 Oct	1	-	16.142	-	-	-
1970 <sup>1</sup>	107	12 Sept-28 Dec	4 Nov	21 Oct	1	-	214.897	-	-	-
1971	107	10 Sept-26 Dec	2 Nov	15 Oct	5	1.555-194.961	104.555	80.715	48.390	7.396
1972	103	16 Sept-28 Dec	6 Nov	22 Oct	5	0.539-405.182	147.184	161.803	42.289	13.748
1973	111	9 Sept-29 Dec	3 Nov	25 Oct	5	56.061-3525.478	1283.245	1421.245	475.964	6.854
1974	85	28 Sept-22 Dec	9 Nov	2 Nov	4	7.097-1880.281	774.356	799.784	259.764	11.848
1975	98	20 Sept-27 Dec	8 Nov	30 Oct	4	3.171-1116.267	340.938	525.348	69.022	12.568
1976	29	10 Oct-8 Nov	24 Oct	24 Oct	3	-	0.518	-	-	-
1977	74	1 Oct-14 Dec	7 Nov	24 Oct	3	5.584-141.235	73.410	-	28.083	-
$\bar{x}$	96.3	19 Sept-24 Dec	6 Nov	25 Oct						
S.D.	14.2	9.1	5.6	6.3						

<sup>1</sup>Season dates based on average of 1971-73 seasons.

<sup>2</sup>1971-1977 seasons, not including 1976 season.

Table 5. Example of computer program used to estimate duration-corrected abundance of herring larvae by length groups and their mean ages for the 1973 season (September 1973-February 1974), Georges Bank-Nantucket Shoals area. The expanded area and day method of Sette and Ahlstrom (1948) was used to estimate abundance of larvae by length groups. An exponential growth model was used to determine duration and mean age from hatch. A mean daily growth increment of 0.195mm/day was used in the model over a length range of 6.5 to 30.4mm. Larvae in the 4-6mm length group were assigned a duration of 10.3 days, thus a mean age of 5.06 days.

Size class midpoint (mm)	Estimated abundance ( $\times 10^{-9}$ )	Duration (days)	Corrected abundance ( $\times 10^{-9}$ )	Mean age (days)
4-6	120342	10.3030	11680.3	5.06000
7	84247	10.3030	8176.93	15.9479
8	32796	9.00406	3642.36	26.5571
9	17446	7.99621	2181.78	35.9151
10	15575	7.19142	2165.78	44.2861
11	16915	6.53389	2588.81	51.8585
12	15290	5.98658	2554.05	58.7717
13	11383	5.52391	2060.68	65.1311
14	11250	4.78444	2351.37	76.5006
16	14547	4.48431	3243.98	81.6283
17	13395	4.21962	3174.46	86.4449
18	10480	3.98444	2630.23	90.9862
19	7309	3.77410	1936.62	95.2819
20	7779	3.58486	2169.96	99.3572
21	5236	3.41369	1533.82	103.234
22	3525	3.25812	1081.91	106.930
23	1783	3.11612	572.186	110.461
24	981	2.98598	328.536	113.843
25	446	2.86627	155.603	117.086
26	360	2.75580	130.634	120.202
27	222	2.65352	83.6624	123.201
28	237	2.55857	92.6300	126.090
29	181	2.47017	73.2742	128.878
30	106	2.38768	44.3945	131.572
31	8	2.31053	3.46241	134.177
32	5	2.23820	2.23394	136.699
33	33	2.17026	15.2055	139.144

Table 6. Estimates of initial larval herring production and mortality rates for the Georges Bank - Nantucket Shoals area, 1971-77 seasons. Initial production of larvae is based on the Y-axis intercept at time zero (6.5 mm S.L.) from the exponential regression of duration-corrected abundance (by method of Sette and Ahlstrom 1948) against estimated mean age in days. The slope of the exponential regression is used to determine the average mortality coefficient (-Z) and percentage rate of decline for two periods, September-December, and September-February. Larvae in the 4-6 mm length group are always underrepresented in the samples and were not considered in the mortality estimation.

Season	Y-intercept value larval abundance Sept.-Dec. ( $\times 10^{-11}$ )	95% confidence interval	Mortality coefficient (-Z) Sept.-Dec.	95% confidence interval	Mortality rate $(1-e^{-Z}) \times 100 = \%/day$	Mortality coefficient (-Z) Sept.-Feb.	95% confidence interval	Mortality rate $(1-e^{-Z}) \times 100 = \%/day$
1971	32.98	2.35-463.06	0.0320	0.0166-0.0475	3.15	(no February Survey)		
1972	119.14	10.44-1360.26	0.0491	0.0338-0.0644	4.79	(no February Survey)		
1973	343.37	26.40-4465.20	0.0481	0.0332-0.0629	4.69	0.0498	0.0347-0.0649	4.86
1974	196.70	25.78-1501.53	0.0436	0.0312-0.0560	4.26	0.0395	0.0319-0.0471	3.87
1975	146.32	19.05-1123.99	0.0538	0.0413-0.0662	5.24	0.0277	0.0190-0.0364	2.74
1976	0.08	0.01-0.66	"0"	(See footnote)	"0"	"0"	(See footnote)	"0"
1977	9.78	1.14-84.08	0.0329	0.0186-0.0472	3.24	0.0355	0.0271-0.0432	3.49

The 1976 season's regression was not significant; initial abundance of larvae underestimated - see text.

Table 7. A comparison of various initial production estimates of herring larvae ( $\pm 10$  mm standard length) for the combined Georges Bank - Mantucket Shoals and separate subareas for the seasons 1968-77. All larval abundance estimates are expressed as  $\text{m}^2 \times 10^3$  larvae.

Season	Area	Stimpson (1959) method		Sette and Ahlstrom (1948) Method	
		(uncorrected)	(4-9 mm size classes)	(Uncorrected)	Duration corrected Mortality and Duration Corrected (4-9 mm size classes)
1968	Mantucket Shoals	-	-	-	-
	Georges Bank	-	-	-	-
1969	Mantucket Shoals	-	-	-	-
	Georges Bank	-	-	-	-
1970	Mantucket Shoals	-	-	-	-
	Georges Bank	-	-	-	-
1971	Mantucket Shoals	6	7.00	0.81	2.23
	Georges Bank	154	106.00	19.97	48.51
1972	Mantucket Shoals	196	330.00	37.62	110.66
	Georges Bank	34	57.00	6.48	18.85
1973	Mantucket Shoals	844	1024.00	104.50	200.16
	Georges Bank	1256	1524.00	152.32	253.65
1974	Mantucket Shoals	249	239.00	24.16	44.92
	Georges Bank	1351	1298.00	135.06	281.67
1975	Mantucket Shoals	336	411.00	42.41	86.72
	Georges Bank	151	185.00	19.54	43.76
1976	Mantucket Shoals	0	0.00	0.00	0.00
	Georges Bank	0.19	1.11	0.13	0.45
1977	Mantucket Shoals	68	80.00	9.04	25.83
	Georges Bank	0.1	0.10	0.02	0.04
	Combined area	68	80.10	9.06	25.87

<sup>1</sup> Abundance of larvae ( $\pm 10$  mm) initially corrected for stage duration as determined by growth model for individual size classes (4-6, 7, 8, 9 mm). Each size class was then corrected to original estimated abundance at zero mean age (3.5 mm) using an average mortality rate,  $Z$  of  $-0.04356$  over time ( $t$ ) in days from the growth model, and then the individual size class estimates summed for the total abundance estimate.

<sup>2</sup> Abundance of larvae in the 4-9 mm size class were first corrected for stage duration using an average value of 9.7 days, and then corrected to initial abundance at zero mean age (3.5 mm) using an average mortality rate,  $Z$ , of  $-0.04356$  over time ( $t$ ) of 21.3 days from hatching, the mean age of the 4-9 mm size class.

Table 7 (continued)

Arithmetic Mean (Uncorrected)	Saville (1955) Method <sup>2</sup>		Y-Intercept Method		
	Duration Corrected (4-9 mm size class)	Mortality and Duration Corrected (4-9 mm size class)	Geometric Mean Uncorrected (4-9 mm size class)	Duration Corrected Abundance (Sept.-Dec.) (> 7 mm size classes)	Range of Estimates
7.56	-	-	-	-	-
51.73	-	-	-	-	-
59.30	6.14	15.43	-	-	6.14 - 59.30
1.04	-	-	-	-	-
15.10	-	-	-	-	-
16.14	1.67	4.20	-	-	1.67 - 16.14
65.05	-	-	-	-	-
149.90	-	-	-	-	-
214.90	22.76	55.93	-	-	22.26 - 214.90
4.67	-	-	3.02	-	-
102.15	-	-	35.65	-	-
104.56	10.03	27.21	48.37	32.98	10.83 - 193.00
151.35	-	-	37.07	-	-
28.06	-	-	7.43	-	-
147.18	15.25	38.31	42.29	119.14	15.25 - 387.00
673.62	-	-	272.27	-	-
732.37	-	-	317.69	-	-
1283.29	132.93	333.98	475.96	343.37	132.93 - 2548.00
111.01	-	-	48.64	-	-
663.35	-	-	158.13	-	-
774.36	80.22	201.53	259.76	196.73	80.22 - 1600.
248.09	-	-	20.94	-	-
92.81	-	-	36.06	-	-
340.94	35.32	88.73	69.02	146.32	35.32 - 596.00
0.00	-	-	-	-	-
0.52	-	-	-	-	-
0.52	0.05	0.14	-	0.08	0.05 - 1.11
73.35	-	-	27.04	-	-
0.14	-	-	-	-	-
73.41	7.60	19.10	28.08	9.78	7.60 - 80.10

Table 8. Abundance, mortality and growth estimates for Georges Bank-Nantucket Shoals herring larvae during five winters.

Survey middate	Estimated abundance ( $\times 10^{-11}$ )	Percentage loss	t(Days)	Instantaneous mortality rate ( $1 - e^{-Z} \times 100 = \%/\text{day}$ )	Duration corrected abundance ( $\times 10^{-11}$ )	Instantaneous mortality rate ( $1 - e^{-Z} \times 100 = \%/\text{day}$ )	Mean length (mm)	Percentage gain	Mean daily growth increment (mm/day)	Specific growth (L) <sup>1</sup> (%/day)	Instantaneous growth (W) <sup>2</sup> (%/day)
Dec. 13, 1973	523.36				124.17		16.5				
Feb. 14, 1974	18.70	96.43	64	5.07	4.72	4.98	23.3	29.19	0.11	0.539	2.52
Dec. 13, 1974	571.95				124.34		15.7				
Feb. 14, 1975	30.19	94.72	64	4.50	11.35	3.67	26.9	41.64	0.18	0.841	3.92
Dec. 9, 1975	95.74				23.10		17.2				
Feb. 16, 1976	62.55	34.67	70	0.60	26.95	-	30.8	44.16	0.19	0.832	3.88
Dec. 4, 1976	7.98				2.22		19.9				
Feb. 18, 1977	3.07	61.53	77	1.19	1.37	0.60	32.0	37.81	0.16	0.617	2.87
Dec. 14, 1977	4.43				1.43		23.1				
Feb. 24, 1978	2.29	65.92	73	0.90	1.05	0.42	32.8	29.57	0.13	0.479	2.23

<sup>1</sup>Based on successive mean lengths (L),  $g = \frac{\ln L_1 - \ln L_0}{t} \times 100$

<sup>2</sup>Based on dry weight (W) of larvae at mean length (L). Length-weight relationships calculated from Chenoweth's (1970) data, Table 2, p. 1877:  $\log W = 4.66 (\log L) - 5.73$

Table 9. A comparison of potential herring egg production for the Georges Bank-Nantucket Shoals area, 1968-77 seasons, determined from VPA stock size estimates and larval survey data. Age specific maturity and fecundity data were used to estimate potential egg production of VPA stock size structure. Initial production of herring larvae was determined by two methods, Saville (1956) and Sette and Ahlstrom (1948), and applying an assumed 10% egg bed mortality correction factor to estimate potential egg production.

Season	VPA Adult Stock Estimate of Eggs Produced ( $\times 10^{-11}$ )	Larval Estimate of Eggs Produced ( $\times 10^{-11}$ ) (method of Saville 1956)	Ratio VPA/Larval Estimate	Larval Estimate of Eggs Produced ( $\times 10^{-11}$ ) (Method of Sette & Ahlstrom 1948)	Ratio VPA/Larval Estimate
1968	2136.60	16.98 <sup>2</sup>	126	-	-
1969	1570.60	4.62 <sup>2</sup>	342	-	-
1970	1182.30	61.52 <sup>2</sup>	19	-	-
1971	906.71	29.93	30	55.81	16
1972	519.71	42.14	12.4	142.48	3.6
1973	363.43	367.38	1.0	499.19	0.7
	(578.81) <sup>1</sup>	367.38	(1.6) <sup>1</sup>	499.19	(1.2)
1974	574.04	221.68	2.6	359.25	1.6
1975	542.30	97.60	5.5	143.57	3.8
1976	415.10	0.15	2767	0.50	830
1977	554.46	21.01	26	28.46	19.5

<sup>1</sup>Estimate of mature female fraction at age 3 of 0.60 used in this case; a value of 0.20 at age 3 used in all other cases

<sup>2</sup>Pre-ICNAF sampling protocols have underestimated larval estimates - see text for details.

Table 10. Comparison of larval herring duration-corrected abundance in February, mean length, overwinter (December-February) instantaneous rates of larval growth and mortality, with relative abundance at age 3 as an index of recruitment for the 1973-1977 year classes. See text for details.

Year class	February larval abundance ( $\times 10^{-11}$ )	February mean length (mm)	Overwinter instantaneous rates(%/day)		Relative abundance at age 3
			Growth	Mortality	
1973	4.7	23.3	2.5	5.0	Poor-Average
1974	11.4	26.9	3.9	3.7	Poor
1975	27.0	30.8	3.9	"0"	Poor
1976	1.4	32.0	2.9	0.6	Good
1977	1.1	32.8	2.2	0.4	

Table 11. Dominant ichthyoplankton collected on larval herring surveys for the 1974-76 seasons. A Biological Index (BI) modified from Fager (1957) was used to rank species based on their station abundances within the separate areas of Nantucket Shoals and Georges Bank. Only dominant species (BI >1) are included in the table.

Species	Nantucket Shoals Survey middate					1974-75		Georges Bank Survey middate				
	14 Sep	07 Oct	24 Oct	19 Nov	13 Dec	14 Feb	14 Sep	07 Oct	24 Oct	13 Nov	13 Dec	14 Feb
<i>Merluccius bilinearis</i>	3.85	1.69	3.55	2.94	1.54	0.00	1.85	2.40	1.60	1.90	0.69	0.00
<i>Urophycis</i> spp.	3.80	3.44	2.45	1.35	0.06	0.00	1.29	2.10	2.69	0.66	0.32	0.00
<i>Citharichthys arctifrons</i>	2.30	1.94	0.86	0.19	0.00	0.00	0.50	0.10	0.19	0.10	0.00	0.00
Ophidiidae	1.45	1.50	0.83	0.02	0.14	0.00	0.46	0.37	0.25	0.00	0.00	0.00
<i>Scophthalmus aquosus</i>	0.20	0.90	1.52	0.76	0.46	0.00	1.38	2.58	2.88	2.12	0.78	0.00
<i>Clupea harengus</i>	0.00	0.00	2.48	4.74	3.60	1.59	0.11	0.17	3.52	4.80	4.81	2.12
<i>Pollachius virens</i>	0.00	0.00	0.05	0.47	1.93	2.66	0.00	0.00	0.00	0.16	1.10	3.13
<i>Gadus morhua</i>	0.00	0.15	0.00	0.18	2.13	1.43	0.00	0.00	0.00	0.30	2.02	2.40
<i>Ammodytes</i> sp.	0.00	0.00	0.00	0.00	0.35	3.93	0.00	0.00	0.00	0.00	0.00	3.15
<i>Melanogrammus aeglefinus</i>	0.00	0.00	0.00	0.00	0.00	0.98	0.00	0.00	0.00	0.00	0.00	1.08

Species	Nantucket Shoals Survey middate					1975-76		Georges Bank Survey middate				
	01 Oct	23 Oct	09 Nov	09 Dec	16 Feb	21 Apr	01 Oct	23 Oct	09 Nov	09 Dec	16 Feb	21 Apr
<i>Merluccius bilinearis</i>	3.17	3.22	3.00	1.44	0.37	0.00	2.37	1.67	1.31	0.48	0.00	0.13
<i>Urophycis</i> spp.	2.43	0.81	0.53	0.17	0.06	0.00	0.80	0.27	0.61	0.00	0.00	0.00
<i>Scophthalmus aquosus</i>	0.78	0.94	0.65	0.00	0.00	0.00	1.70	1.31	1.15	0.00	0.12	0.00
<i>Clupea harengus</i>	0.00	2.44	3.15	2.58	1.69	0.42	0.16	3.33	4.31	3.30	2.44	1.27
<i>Pollachius virens</i>	0.00	0.14	0.21	1.82	0.94	0.40	0.00	0.00	0.07	1.08	2.36	0.23
<i>Gadus morhua</i>	0.00	0.01	0.10	1.52	1.10	1.33	0.00	0.00	0.00	1.75	1.09	1.63
<i>Ammodytes</i> sp.	0.00	0.00	0.00	0.29	5.00	4.58	0.00	0.00	0.00	0.80	4.67	3.66
<i>Melanogrammus aeglefinus</i>	0.00	0.07	0.00	0.00	0.12	0.06	0.00	0.00	0.00	0.00	0.12	1.34
<i>Hyacocephalus otodasomepinex</i>	0.00	0.00	0.00	0.00	0.28	1.02	0.13	0.00	0.00	0.00	0.00	0.86

Species	Nantucket Shoals Survey middate					1976-77		Georges Bank Survey middate				
	08 Oct	24 Oct	22 Nov	04 Dec	19 Feb			08 Oct	24 Oct	22 Nov	04 Dec	19 Feb
<i>Urophycis</i> spp.	3.94	2.90	1.26	0.00	0.00			3.80	2.06	0.64	0.00	0.00
<i>Merluccius bilinearis</i>	3.33	2.70	2.18	2.68	0.00			3.09	1.84	1.18	0.76	0.20
<i>Scophthalmus aquosus</i>	1.77	1.00	0.45	0.40	0.06			2.68	1.36	1.12	0.39	0.00
<i>Clupea harengus</i>	1.44	0.65	1.18	1.36	1.23			0.57	3.23	1.48	1.30	0.60
<i>Citharichthys arctifrons</i>	1.00	1.60	0.74	0.68	0.00			0.66	0.07	0.94	0.13	0.00
<i>Paralichthys dentatus</i>	0.00	1.25	1.42	0.80	0.17			0.08	0.39	0.00	0.00	0.00
Ophidiidae	0.00	1.03	0.11	0.00	0.00			0.96	0.37	0.00	0.00	0.00
<i>Gadus morhua</i>	0.00	0.00	0.00	1.29	0.31			0.00	0.00	0.36	0.56	0.00
<i>Ammodytes</i> sp.	0.00	0.00	0.00	0.20	4.58			0.30	0.00	0.00	0.10	0.90
<i>Notolapia risaei</i>	0.00	0.13	0.21	0.34	0.00			0.41	0.35	0.16	1.02	0.00

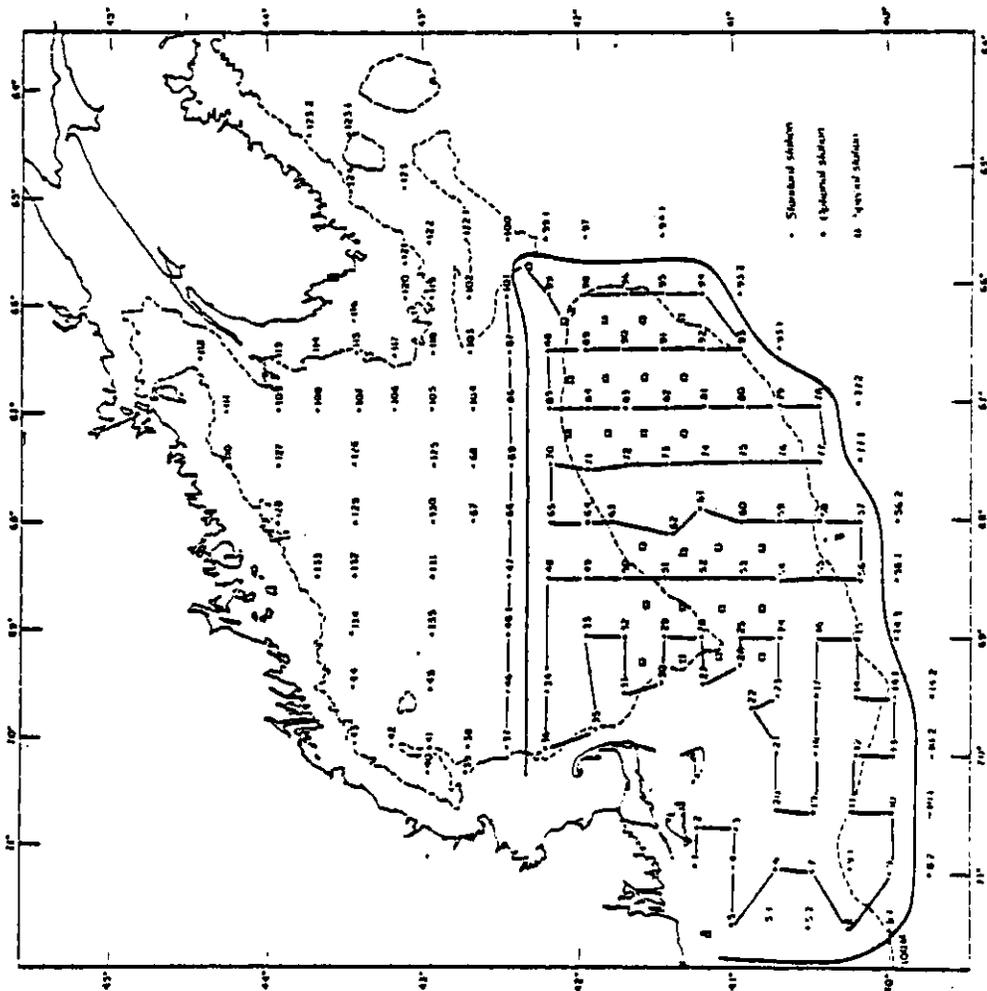


Figure 1. Station plot for ICNAF larval herring surveys with a standard cruise track drawn for the Georges Bank - Nantucket Shoals area. Station sampling within the encircled dark line has been emphasized since 1974, and this area represents our best coverage for the entire larval herring time series. Stations 1-36 represent the Nantucket Shoals area, and Stations 48-99 represent the Georges Bank area. Standard stations (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.

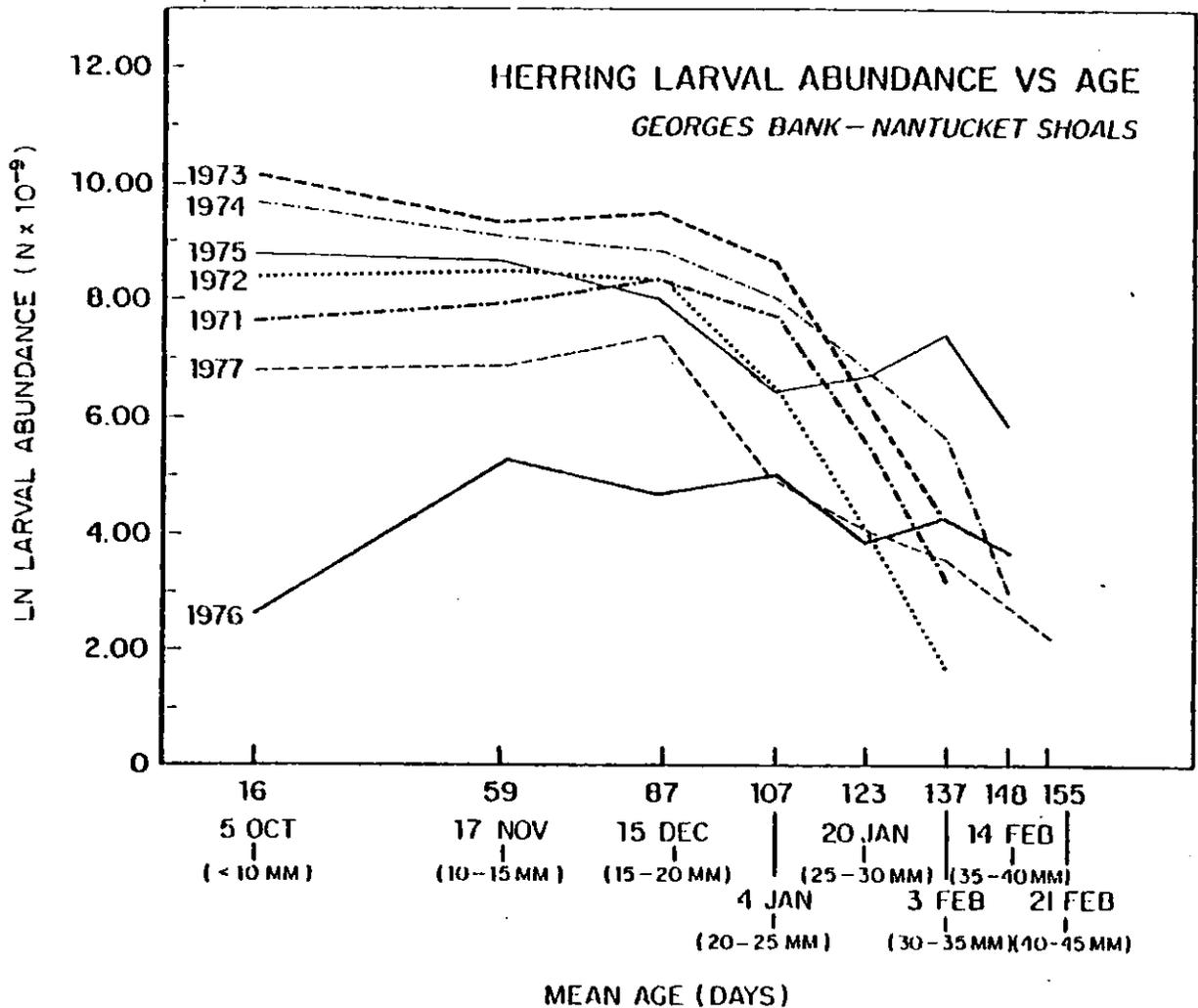


Figure 2. Larval herring duration-corrected abundance versus mean age in days from hatching of the length class given in parentheses for the Georges Bank - Nantucket Shoals area, 1971-77 seasons. A common initial hatching time of 19 September was used to compare the abundance of larvae at mean age of a given length class. The 1976 estimate of <10-mm larvae is probably underestimated by an order of magnitude.

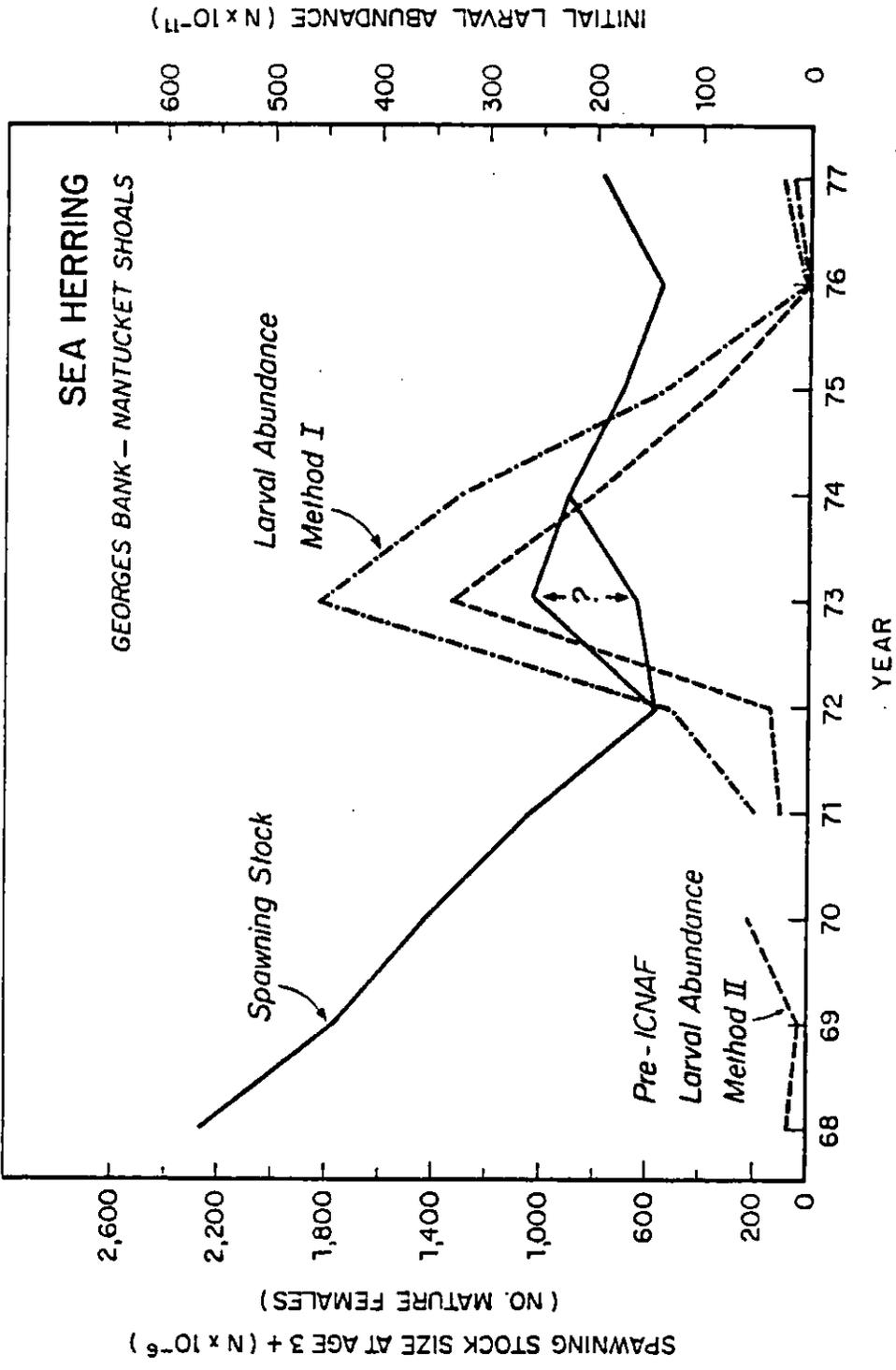


Figure 3. A comparison of herring mature-female spawning-stock size at age 3+ from the most recent VPA estimates with abundance of larvae (<10-m length, duration and mortality corrected to zero mean age at hatch) determined by two methods for the combined areas of Georges Bank and Nantucket Shoals, 1968-77 seasons. Note difference in scales. The number of mature females was based primarily on the geometric mean of the fraction mature at age 3. For the year 1973, the mature fraction of 0.60 at age 3 also was calculated as there is evidence that a large number of 3-year-old herring composed the fishery matured at an earlier age (see text): a question mark denotes these two estimates in the figure. Initial larval abundance estimates were calculated for the years 1971-77 by Method I of Sette and Ahlstrom (1948), and for the years 1968-77 by Method II of Saville (1956). Larval abundance for the 1968-71 and 1976 seasons are underestimated.

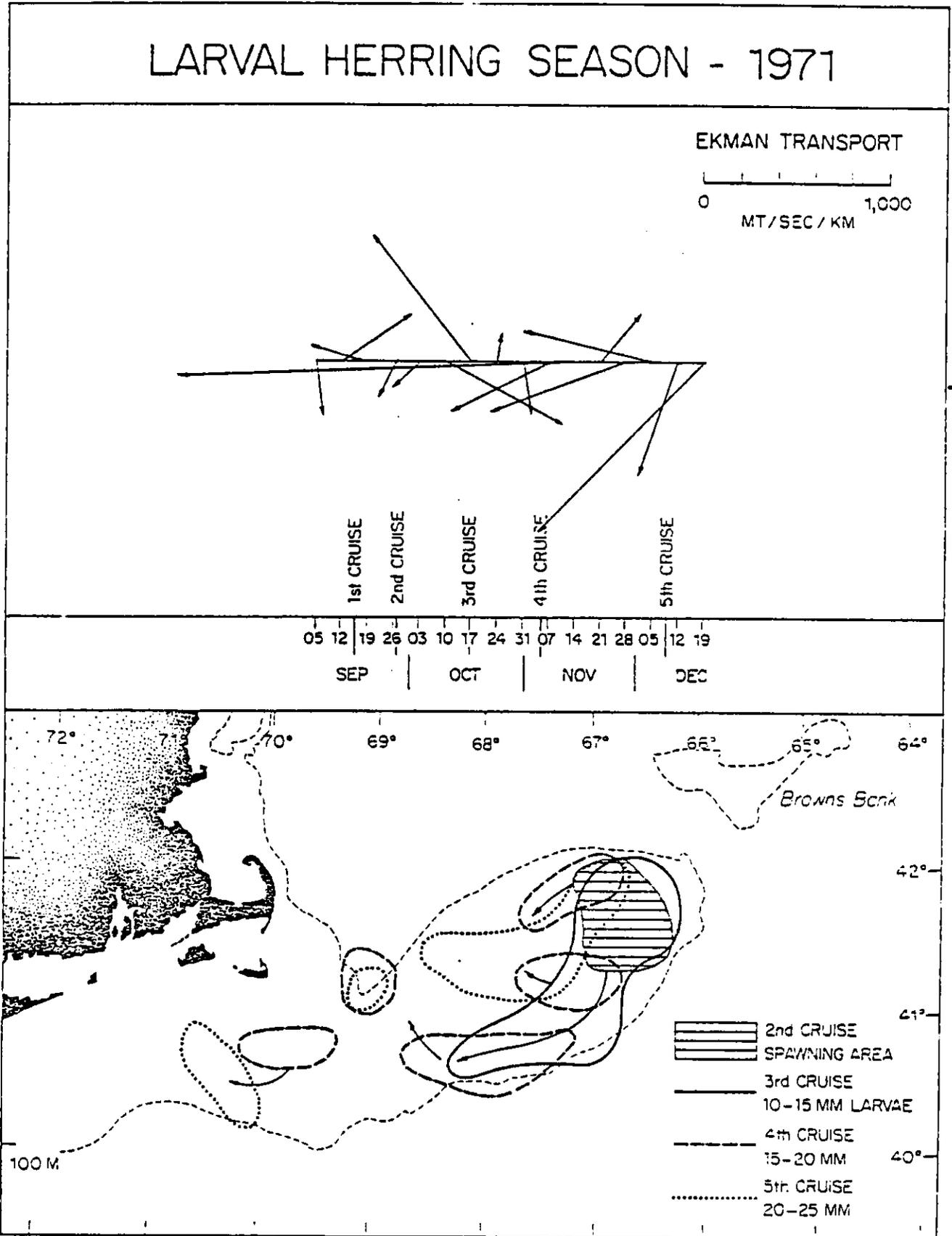


Figure 4. Example of the 1971 season's dispersal of herring larvae between successive cruises and computed weekly Ekman transport.

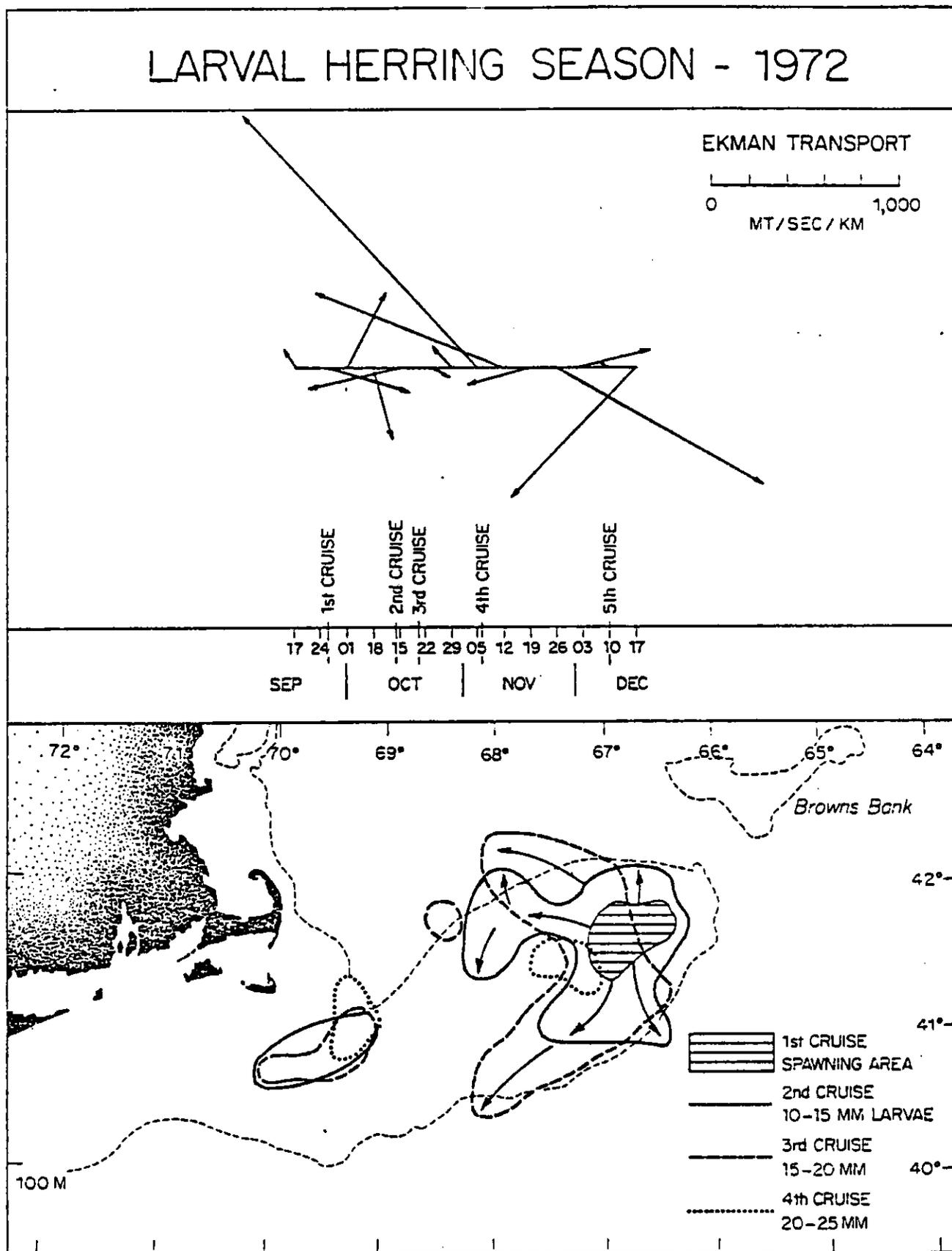


Figure 5. Example of the 1972 season's dispersal of herring larvae between successive cruises and computed weekly Ekman transport.

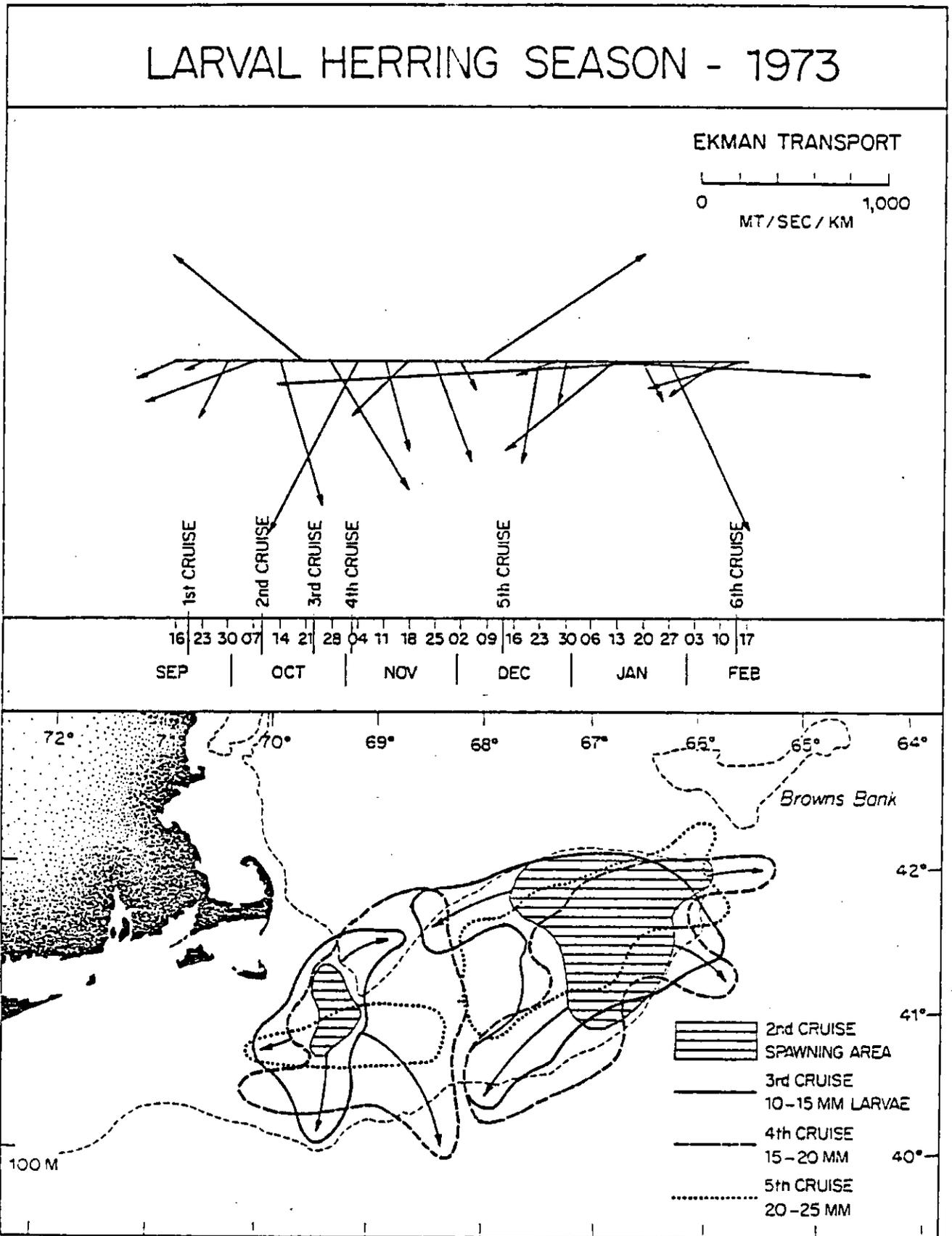


Figure 6. Example of the 1973 season's dispersal of herring larvae between successive cruises and computed weekly Ekman transport.

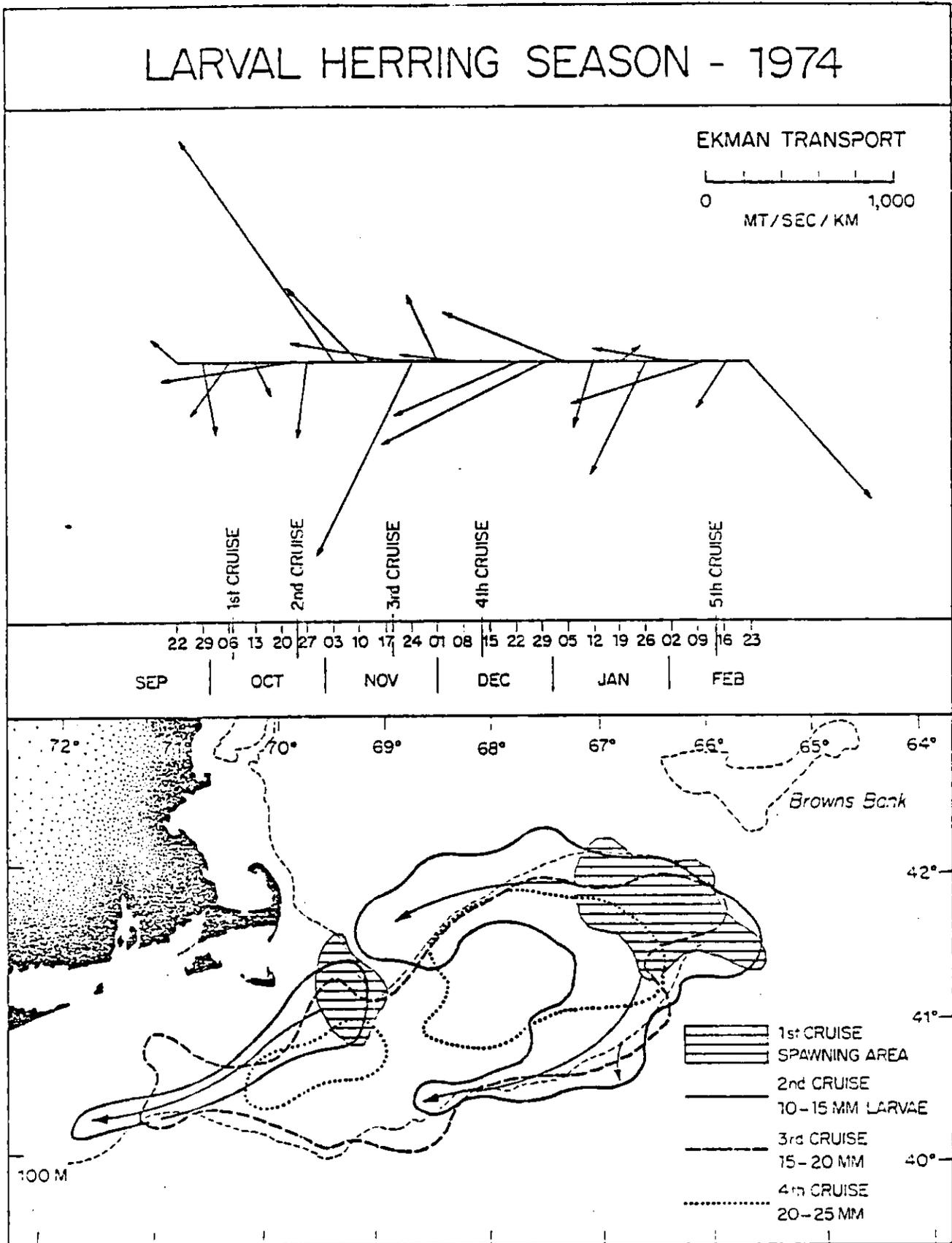


Figure 7. Example of the 1974 season's dispersal of herring larvae between successive cruises and computed weekly Ekman transport.

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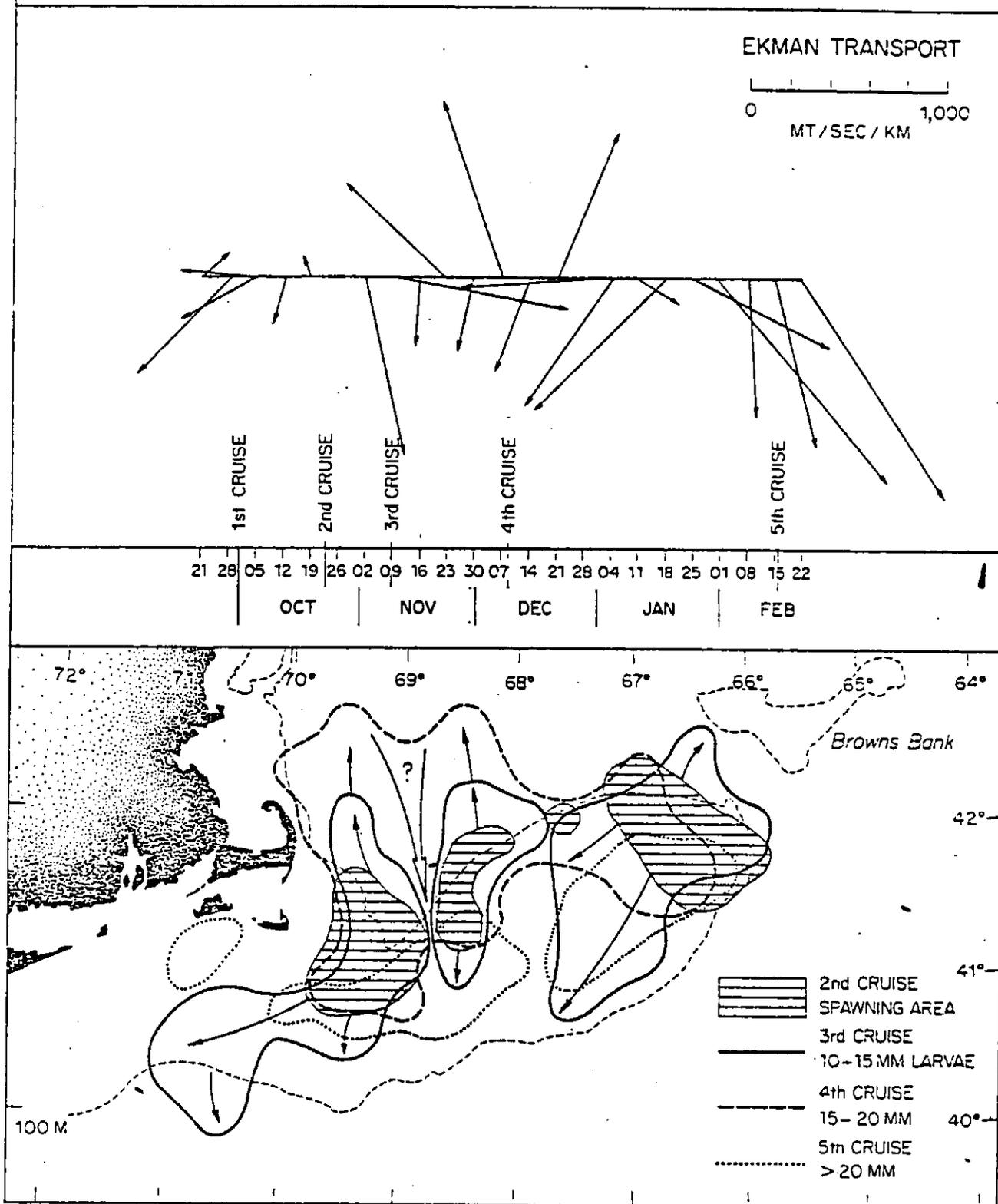


Figure 8. Example of the 1975 season's dispersal of herring larvae between successive cruises and computed weekly Ekman transport.

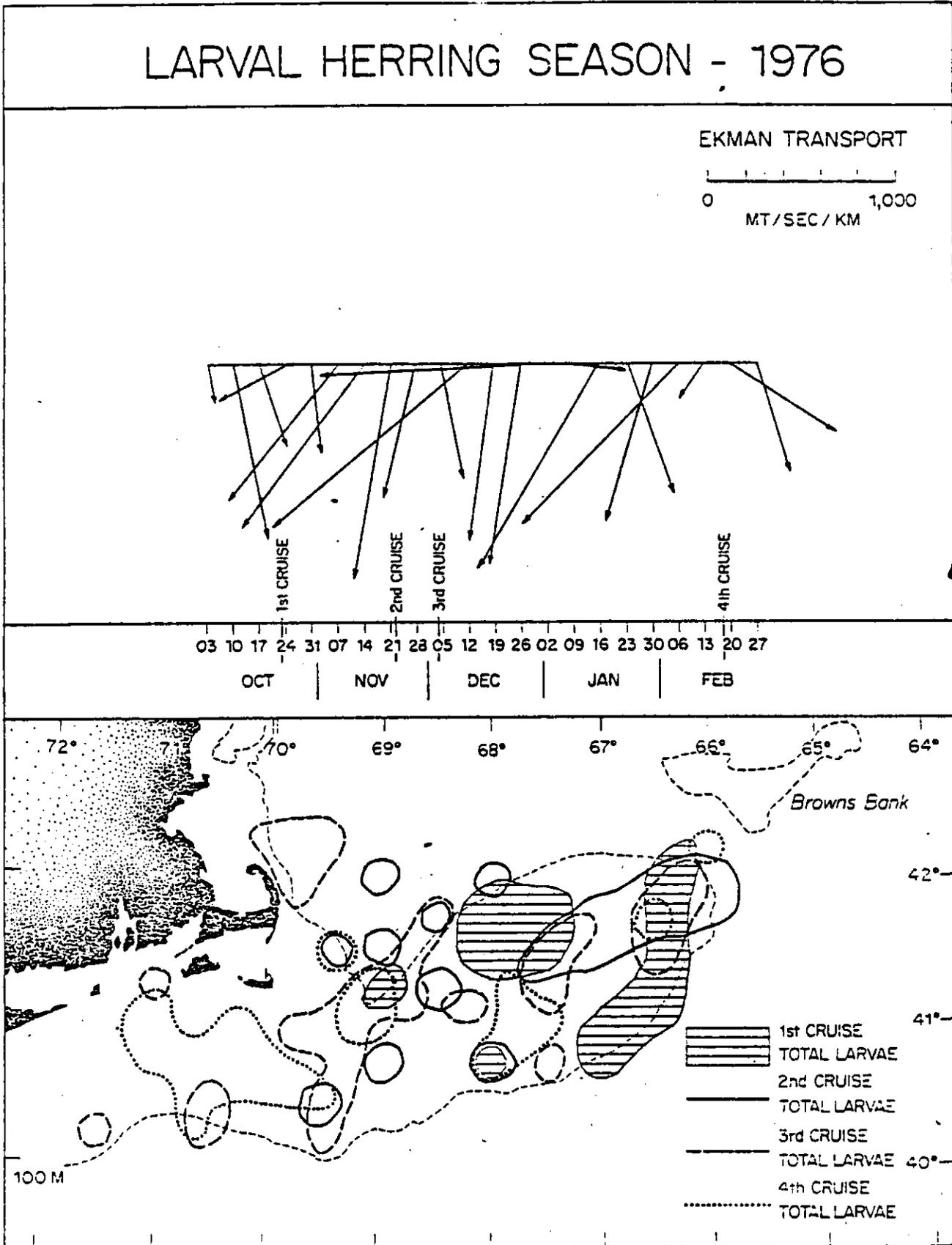


Figure 9. Example of the 1976 season's dispersal of herring larvae between successive cruises and computed weekly Ekman transport.

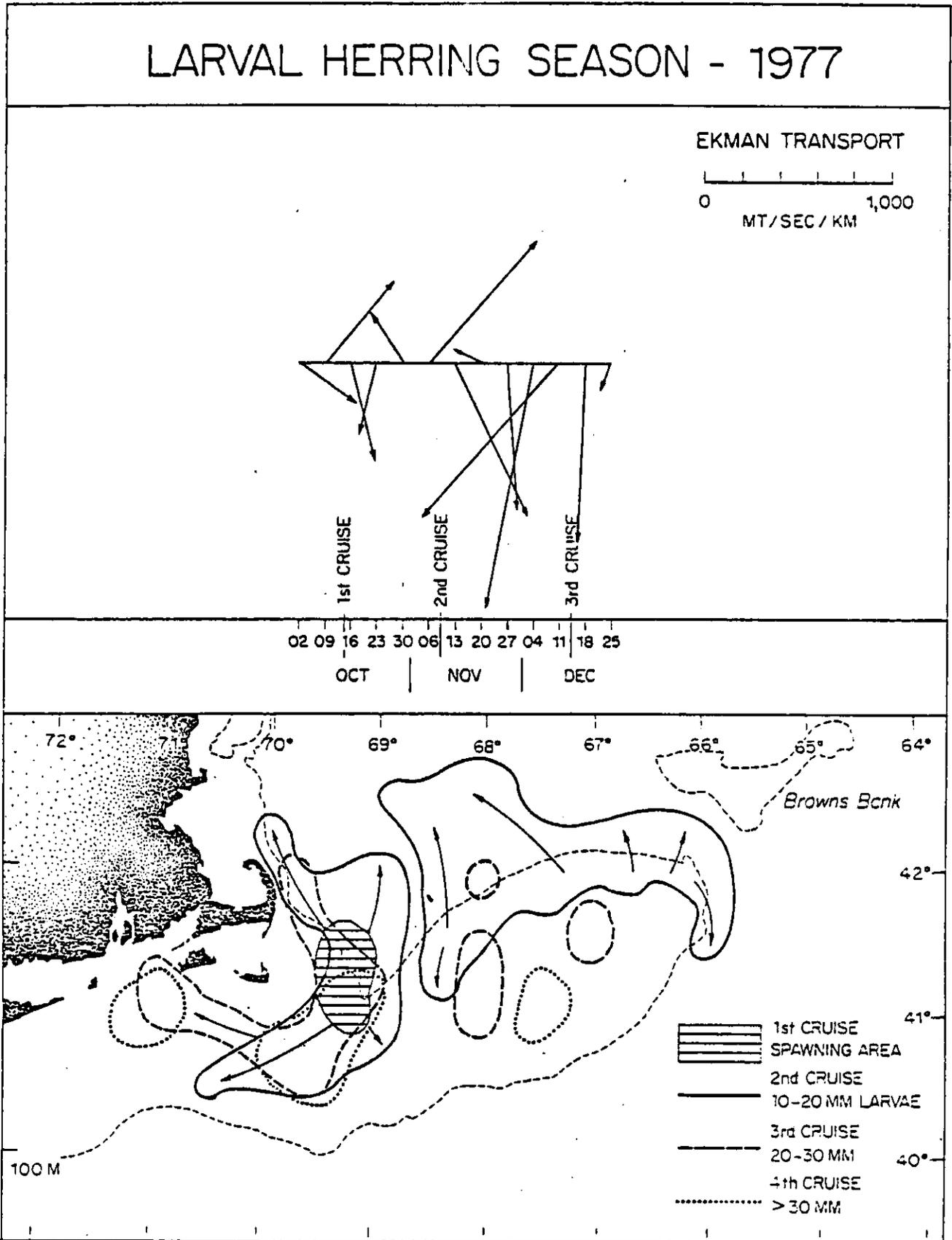


Figure 10. Example of the 1977 season's dispersal of herring larvae between successive cruises and computed weekly Ekman transport.

