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Production of Larval Herring, *Clupea harengus*, along Coastal Maine (1964-1978) and its Relation to Recruitment Mechanisms of the Sardine Fishery

by

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In 1962, research on larval herring was initiated to determine possible relationships between annual larval abundance (or a correlative of abundance) and fluctuating harvests of juvenile herring in the Maine sardine fishery. Research in the 1960's culminated in: 1) a description of the coastal ecology of larval herring, and 2) selection of the winter mortality, the winter condition, and the spring abundance of larvae as being the kinds of estimates most suitable for anticipating year-class strength Graham et al., (1972a). In the 1970's, winter mortalities and springtime standing crops of larvae were monitored. In the late 1970's, winter condition was also monitored.

The assembled results of this fifteen years of sampling culminate in this paper, which includes a model of larval production based on the concepts that: 1) the basic determinants of larval year class strength are the level of larval abundance following a density-dependent phase of mortality in autumn and a density-independent phase of mortality during winter and 2) these basic determinants may be modified by late spawning and the shifting of spawning sites by the adult herring. An attempt is made to link these determinants with recruitment of juvenile herring to the sardine fishery. It is suggested that the success of the coastal herring stocks under stress can be traced to the opportunity of its larvae to distribute themselves efficiently inshore, utilizing these waters as nursery grounds.

METHODS

Larval mortality estimates are based on field samples taken from the Sheepscot River estuary during the winter months of 1964-1973 and 1977. Mortality was determined in the winter because larval movements are reduced during that season and because the relatively harsh environment probably has a significant effect upon the larval population. With the techniques we employ, we are able to sample the relative abundace of larvae discretely from each element of the tidal current system that transports them. Characteristics, performance, and sampling designs for our buoyed and anchored nets have been described by Graham and Venno (1968), Graham and Davis (1971) and Graham (1972a).

From 16 to 32 samples were obtained from the buoyed and anchored nets during each overnight sampling period in the autumn and winter. Essentially, four lines of nets were fished at four stations in the estuarine channel. Each line had four nets attached. During 1965-1967, the gear was set at slack water during dusk, retrieved, and reset at the end of the tidal stage during slack water, and then retrieved before dawn during slack water. The nets fished approximately 6 hours each on the flood and ebb tides, one semidiurnal tidal cycle. These overnight sets yielded 32 samples. During 1964 and from 1968-1978, the catches of the tidal phases were pooled by setting the gear at dusk and retrieving at dawn after the nets fished one semidiurnal tidal cycle. Pooling reduced the number of samples by one half. Prior to 1971, mortality estimates were based upon an overnight sampling period in December and another in January. From 1971 to the present, a second overnight sampling period was added in December and January to compensate for low numbers of larvae captured in the early 1970's. When calculating mortalities, I averaged the catch rates from the two sampling periods for each month. Graham and Davis (1971) have reported mortalities for larval herring from the Sheepscot River estuary for the year classes 1964-1967. They compared mortalities between larval year classes by adjusting all their estimates to 15-daycalendar intervals.

For the instantaneous mortality rates of this paper, I use winter as the unit of time and the number of semidiurnal tidal phases during winter as the environmental time scale. The number of tidal phases appears to be a more realistic scale upon which to base larval mortality than one that is chronological. Tidal and chronological scales do not correspond since four tidal phases exceed one day by 50 minutes. Mortality rates are expressed for the sampling in December and January and for the entire winter. Evidence presented in the results section of this paper suggests that larval mortality in winter might be relatively constant. To obtain an estimate of mortality over the sampling period:

$$N_t/N_o=e^{-zt}$$

where N_o is the catch in numbers per 100 m^3 at the beginning of the sampling period, N_t is the catch t tidal phases later and z is the instantaneous rate of death per tidal phase.

The estimate of winter mortality (a 3-month period) is determined from 372 z since 372 tidal phases occur over a 3-month period from the second week in December to the second week in March.

Estimates of the relative abundance of the larvae were made each spring from inshore and coastal sampling areas located along the Maine coast. Samples were obtained (1965-1979), just before the larvae metamorphosed into juvenile form; presumably, at such a time all critical periods would be completed. The central and long-term, inshore, sampling area extended 24 km shoreward from the headlands into the estuaries and embayments and the coastal sampling area extended 24 km seaward from the headlands. The inshore area contained 8 sampling stations and the coastal area contained 15 (Fig. 1). The location of the sampling stations was intended to overlap eastern and western coastal environments which differ. The timing of the cruises was intended to ensure sampling when a significant portion of the larval population was present during late March to late April. The cruises inshore and along the coast were quasi-synoptic. But, on three occasions in the 1960's either two inshore or two coastal cruises were completed during this period; the catch rates of larval herring for these double cruises were averaged. Samples were obtained using stepped oblique hauls at 4-6 km as described by Graham et al. (1972a) with a Boothbay Depressor trawl. Characteristics and performance of the trawl have been described by Graham and Vaughn (1968) and Graham (1972b).

Special studies determined towing paths and depths appropriate to monitoring larval abundance in the inshore and coastal waters. One such study examined the effects of the lengths of stepped oblique tows upon the capture of larval herring (Graham, 1980a). The results indicated that the long, stepped oblique tow (5.5 km horizontally) used to sample larvae underestimated their abundance at a given station. However, as the larval population increased, the magnitude of the underestimate decreased and did not occur when larvae possibly "saturated" the locality of the station. Under such circumstances, a systematic error was introduced into the data. There was also a tendency to locate sampling stations along towing paths that favored the protection of the net. Possibly, such subjective sampling concentrated on similar limbs of circulation systems along the coast and ignored others (Graham, 1970a). In response to these problems, the coastal area was divided into 30-minute squares of latitude and longitude for sampling, beginning in 1966. Each square was divided into 4 quartiles and a single quartile was selected randomly for sampling. In the selected quartile 2 short tows (1.75 km horizontally) were chosen randomly from among the 4 short tows possible along the track of a potential long tow. The direction of tow was determined randomly and the catch rates of the 2 short tows at each station were averaged. Stratified random sampling was not possible at our inshore stations because of vessel incapabilities and the confining shorelines with their associated rock ledges. Therefore, long tows were continued but the catch rates from inshore cruises and from a 1965 coastal cruise were adjusted using the following relationship determined experimentally (Graham, 1980a):

$\hat{Y} = .601 + .793\ X$
$r = .71$

Where $\hat{Y}$ is the estimated mean catch rate ($\log_{10}$) from two short tows and X is the catch rate from a given long tow ($\log_{10}$). r is the correlation coefficient, P.01 = .42

The adjusted catch rates increased the agreement of some relationships given below, but did not affect the conclusions reached.

In view of the rugged coastal bottom, sampling was not extended to depths exceeding 20 m in coastal water. To determine the possible effect of this limitation, a study examined the depth distribution of larvae in the spring of 1967 (Graham, 1980b). Samples were collected only during daylight, as during cruises. The experimental results suggested that a large aggregation of larvae, when present at a station, would be captured by our shallow tow during a dull day. On a bright day the aggregation would be below 20 m and would be missed by our towing path. Thus, on a dull day our catch would overestimate the abundance of larvae at a given sampling station and on a bright day underestimate it.

The extinction of light in the upper coastal water varies considerably from place to place (Graham, 1970b). Thus, it is difficult to discern what constitutes a dull or bright day to larvae from the various stations. Hopefully, the randomization introduced both purposefully and inadvertently by the sampling procedures will mitigate any systematic effects upon the mean larval catch rate per cruise.

In the spring, land masses funnel and concentrate the larvae as they move up the estuaries and embayments. Thus, the probability of capturing larvae from the inshore region during migration may change at a rate different from that of the coastal region. Therefore, we combined the mean catch rates from the inshore and coastal stations to produce an index of larval abundance.

In 1973, monitoring was extended to eastern Maine and in 1974, to western Maine (Fig. 2). Although most of the areas of coastal water in the three sampling systems (eastern, central and western) were sampled, it was not feasible to sample completely the many estuaries and embayments. The inshore areas chosen for sampling were assumed to be representative of the others.

Procedures for assessing larval condition were those given by Chenoweth (1970) who used the relative condition of LeCren (1951) where:

$$\text{relative condition} = \frac{W}{\hat{W}}$$

and W is the observed weight in milligrams of larvae for each millimeter interval of length and $\hat{W}$ is the estimated weight of larvae for each millimeter interval calculated from the regression of log weight against log length on the data from each year class.

RESULTS

Winter Mortality. Catch data for the Sheepscot River sampling (1964-1973 and 1977) are presented in Table 1. Mortality estimates for the year classes of 1964-1973 and 1977 are given in Table 2. Estimates for the year classes of 1974-1976 were not made because the larvae of those three years migrated into the estuary during winter. The absence of such a migration was a fundamental requirement of the experimental design (Graham and Davis, 1971). The year classes of 1964, 1969, 1970 and 1977 all suffered winter mortalities in excess of 90%. Winter mortalities of the 1967, 1968, and 1973 year classes exceeded 80%; those of the 1966 and 1972 year classes were above 70%. Larvae of 1971 suffered mortality slightly greater than 30%, which was the only relatively low mortality in 11 years.

Spring Abundance. The spring abundance (mean catch per 100 m^3 totalled over coastal and inshore areas) in the central sampling system became progressively more variable for larvae hatched during 1965-1978 (Table 3). The abundance indices declined for year classes 1965-1968, followed by a relatively low index in 1969. Moderate indices were obtained for the 1970-1972 year classes, although the index for the 1971 year class was realtively high. But, for year classes 1973-1978 the indices alternated between relatively high and low values involving the lowest (1978) and the highest (1976) values obtained for the 14 year classes (Table 3).

Spring abundance estimates of the 1970's for eastern and western Maine also displayed considerable variation, but some possible relationships among them emerged. During the first 5 years of sampling, the index of abundance from central Maine usually exceeded that of eastern Maine and during the first 4 years (Table 3) those of western Maine. However, this trend was disrupted by the 1978 year class of larvae. These larvae produced the lowest catch recorded during the 14 years of sampling in central Maine and the highest value during the 6 years of sampling in eastern Maine.

Support of Estimates. A plot of the spring abundance indices against the winter mortality estimates (Fig. 3) suggested that for year classes 1965-1973 and 1977 a higher winter mortality preceded a lower larval abundance in the spring. An inverse relation between spring abundance and winter mortality would be expected and in this sense Figure 2 supports the validity of the estimates of winter mortality.

Although the estimates of mortality were made in the first half of winter, the agreement suggested in Figure 3 would also indicate that during the remainder of the winter season larval mortality might be either constant or changed at the same rate each year. For this reason, calculation of seasonal mortality rates appeared practicable. (The possibility that larvae from offshore also contribute to the spring catch, but do not alter the relationship in Figure 3, is considered in the DISCUSSION section).

Changes in Larval Movements. During 4 of the 15 years of sampling, larval herring moved into the Sheepscot River estuary (Fig. 1) in the winter as well as in the autumn. From 1964-1973 larval herring moved into the estuary during autumn but slowed or ceased such movement by early December. Larvae of the 1974 year class moved into the estuary during mid-December as well, and those of the 1975 and 1978 year classes did so in early January. Larvae of the 1976 year class appeared in the estuary as late as February. The timing of larval movement returned to its former pattern in 1977.

These changes in larval movement are illustrated in Figures 4-10 (which show contours of larval catch rates by larval size over time). The figures indicate when the larvae entered the estuary and whether the entering larvae differed in size from those already present. Two examples of early data (1965-1966) are presented in Figures 4 and 5. They are typical of data from years 1964-1973 when larval catch rates reached a peak in the autumn and declined in winter (unpublished data, autumn data are not available for 1971). Five years of change (1974-1978) are shown in Figures 6-10.

Catches of larvae declined with a uniform increase in size after early December for year classes 1965-1966 and 1977. Relatively small larvae of year classes 1974-1975 entered the estuary in mid-December and January, respectively. Many of these larvae were the same size as those present in the estuary 1-2 months earlier. Four successive larval groups from the 1976 year class entered the estuary but the larvae of each successive group was larger than its predecessor (Fig. 8). Catch rates of the 1978 year class were very low for all larval lengths throughout the autumn and winter, compared to previous years. A winter movement of the larvae into the estuary was not readily apparent. However, a study of the otoliths of the larvae of this year class suggested that the slight increase in catch rates over the larval size range in January and February was caused by an inshore movement of larvae hatched later than those present in November (Townsend and Graham, MS).

Larval Condition. The data in Table 4 and Figure 11 support the previous findings of Chenoweth (1970) that larval condition in the inshore area of this study (Fig. 1) varies with season, and the data also indicate that larval condition may vary with catch rate. Chenoweth (1970) reported that larval condition was relatively better in autumn and spring than in winter when poor condition was at times associated with relatively high larval mortality. On the average, larvae of the 1976 year class (Table 4) had higher condition factors in the autumn (1.270) than in winter (.884). Similarly, the 1977 and 1978 year classes had higher average, autumnal factors in autumn than in winter. In 1977, the average, autumnal factor was 1.133 and for winter 1.047; in 1978, 1.032 and 1.016 respectively. A meaningful, statistical comparison of these trends among sampling years was precluded by the changes in larval movements during winter. From October 1976 to March 1977, four peaks in larval catch occurred (Fig. 11); one each on 18 October, 29 November, 20 December, and 7 February. However, the peaks of 29 November and 20 December were poorly separated by the isolines of catch in Figure 8 suggesting that the latter peak might represent a relatively small addition to the larvae already in the estuary. Each peak in catch, and in one case a double peak, accompanied a decline in larval condition. From October 1977 through February 1978 there was a single peak in catch, on 20 October. Although the peak appeared to accompany a decline in relative condition, only three sampling periods were available and the data were inconclusive. From late November 1977 through February 1978 there were no peaks in catch and no easily discernible trend in larval condition. Rather there was increased variation in larval condition as winter progressed and a low in February. On the average the relative condition of the larvae decreased through winter; 1.085 (Dec.), 1.051 (Jan.), and 1.006 (Feb.). Although the decrease is slight, these observations agreed with data collected previously by Chenoweth (1970) within the inshore area (Fig. 1). He also obtained a monthly reduction in condition factor during 1964-1967, when larvae did not enter the estuary in winter. A relation between catch rates and condition factors of the 1978 year class was discernible although not as precisely as for the 1976 year class. Each of the rather small peaks, one in November and the other in January, were accompanied by a decline in the condition factor. The relatively low condition factor on 5 October was calculated from only 6 fish (Table 4) and perhaps it is unreliable.

Larval and Juvenile Herring. In this section, the indices of larval abundance and survival are compared with the catches of herring in the juvenile fishery of Maine, under the assumption that the commercial catches are valid indices of juvenile abundance (Fig. 12). Such an assumption appears justified. Anthony (1972) suggests that an adjusted index of juvenile abundance corresponds closely to the total catch of fixed gear (stop seines and weirs) of the Maine coast. However, the fishery is influenced to an unknown degree by the availability of the herring to these gears, and although the 2-year-old herring are the mainstay of the fishery, the combined catch of 1-, 2- and 3-year-old herring is also plotted in (Fig. 12) in an attempt to reduce any possible effect of availability.

A comparison between larval catches in the winter and spring, larval survival, and the weight and number of juveniles captured for year classes 1964-1978 is plotted in Figure 12. The close agreement between winter survival and subsequent spring catch was again apparent for larval year classes 1965-1973 and 1977. But spring catches of year classes 1974-1976 and 1978 fluctuated widely and measurements of survival were not feasible because larvae moved into the estuary during winter. The winter catches declined generally for year classes 1964-1973 which did not agree with winter survival and the spring catch after 1969. Winter catches for 1974-1976 year classes were especially large because of the movement of larvae into the estuary during winter. In 1976, the winter movement involved at least two groups of larvae and was followed by a spring larval catch twice that of the other year classes. There was general agreement among larval survival, larval spring catch and the juvenile catch for year classes 1964-1969 with a decline to a low for the 1969 year class. A slight rise in these larval indices coincided with a relatively large rise in the juvenile catch for the 1970 year class. But the large rise in survival and spring catch recorded for the 1971 year class was not reflected in the juvenile catch. Those year classes (1974-1976) having a winter movement into the estuary also had an increase in the juvenile catch over the preceding three year classes (1971-1973). The larval catch rates of the spring and the juvenile harvest in Figure 13 were divided into two groups to illustrate subjectively the tendency for these two quantities to agree for early year classes, 1965-1970, and to disagree for later year classes, 1971-1977.

Agreement among the larval indices and the juvenile harvest was difficult to obtain over an extensive series of years except in one instance. A statistically significant correlation held for the winter (December) larval index of abundance and the catch of juvenile herring (Fig. 13). The correlation is improved when the larval catch per 100 m^3 in December was multiplied by larval survival for the remaining winter, thus forming an index of the effect of winter mortality on the initial standing crop (Table 5, Fig. 13). However, the statistical significance depends heavily upon a single point (1966 YC) and values for the 1968 and 1970 year classes depart considerably from the regression line.

Perhaps the harvests of the 1968 and 1970 year classes are unusual compared to the harvests of other year classes since they also do not agree with the abundance of adults on Georges Bank. Anthony and Waring (1978) ran multiple regressions on age 2 and 3 catch data from the Maine juvenile fishery against data on adult fish from Georges Bank to predict recruitment to Georges Bank. Although they obtained a statistically significant relationship, the prediction equation overestimated the abundance at age 3 of the 1968 year class by 82%, the 1969 year class by 64%, and underestimated the 1970 year class by 58%. They did not offer an explanation for the overestimates of the 1968-1969 year classes, but suggested that the coastal harvest of the 1970 year class might have been even higher had not the herring remained offshore (as reported by fishermen) where they were not available to the inshore fishing gear.

Although peak autumnal catch rate was not chosen as a reliable index for monitoring larval abundance, some comment concerning its relation to the harvest of juveniles is appropriate. During the years 1965-1970 and 1973-1976, when autumnal sampling was undertaken, an average catch rate of 23.34/100 m^3 involving 3420 larvae was obtained. Extreme rates during those years were 7.10/100 m^3, 1456 larvae; and 55.27/100 m^3, 4387 larvae. A relation between peak catch rates and the catch of the juvenile fishery was not apparent until 1977. The extreme catch rate (79.40/100 m^3, 36798 larvae) preceded a large harvest of 1- and 2-year-old herring by the fishery. The harvest of 747 million fish from the 1977 year class was exceeded only by that of the 1966 year class (Fig. 13). In 1978, larval samples revealed the lowest peak catch rate (4.39/100 m^3, 1133 larvae) for the sampling period. Catch records of 1980 and 1981 may reveal whether this low catch rate will affect the harvest of the juvenile fishery. Possibly, such an effect would be localized since the spring estimate of larval abundance for the 1978 year class was low only in central Maine (Table 3).

DISCUSSION

Mortality. Two types of mortality may be important features of the ecology of larval herring in the Sheepscot estuary during the autumn and winter. The first may be induced by overcrowding of the larvae and the second may reflect only the vicissitudes of the environment. This is suggested by the data on indices (catch rates) of larval abundance and relative condition shown in Figures 4-11.

Peaks in larval abundance occurred when larvae moved into the estuary in autumn and, during some years, in the winter as well (Figures 4-8). During the autumn and winter of 1976-1977, a series of peaks occurred (Figures 8 and 11), which perhaps caused overcrowding of the larvae within the estuary and subsequent mortality. This was indicated by the data on relative condition shown in Figure 11; each increase to a peak in abundance accompanied a decline in the relative condition of the larvae. This apparent relation between indices of abundance and condition suggested an explanation for the sharp decline following each peak in abundance. Early migrants entering the estuarine channel had perhaps a relatively high condition factor. As a major aggregation of larvae entered, the channel became overcrowded and through intraspecific competition the larvae lost weight. Interspecific competition probably did not occur; few other larval fishes were present in the autumn and during most of the winter. Since larval herring were not known to move out of the estuary in the autumn and winter, the decrease in abundance perhaps indicated that their mortality was associated with debilitation from loss of weight. Chenoweth (personal communication) kept larval herring in a tank in which they starved and died. He found the appearance of these larvae to be similar to those larvae with low condition factors taken from the inshore area. With the reduction of larval abundance to a low level, possibly intraspecific competition was no longer important to larval survival. The surviving larvae would then regain the higher condition factor exhibited when entering the estuary. With the entrance of a new larval aggregation, the cycle would be repeated.

The larval condition factor did not exhibit trends in the absence of winter peaks in catch, but the relatively low larval condition of winter may be associated with winter mortality. Chenoweth (1970) obtained a reduction in the monthly condition factor for larval year classes 1964-1967. I compared this reduction to winter mortality estimates made in the Sheepscot River estuary for the same year classes and obtained a reduction in the condition factor with an increase in winter mortality estimates (Graham and Davis, 1971). I later (Graham et al., 1972a) extended this comparison to include the 1968 and 1969 year classes. Data from the 1968 year class agreed with the previous comparison, but data from the 1969 year class did not.

The causes of winter larval mortality in the estuary are not known. Cold lethal temperature was indicated for the 1964 year class (Chenoweth, 1970; Graham and Davis, 1971) and starvation was considered for other year classes because of a general reduction of larval food during winter (Sherman and Honey, 1970). Sherman (personal communication) reported a parasitic nematode in the larvae of the inshore area which might debilitate or kill them. Dow (1976) suggested that temperature has been the principal long term environmental regulator of species abundance and availability, including herring, in the Gulf of Maine. Whatever the causes, the winter mortality may be a critical determinant of the size of the larval year class of the subsequent spring just before metamorphosis (Fig. 3).

The two types of mortality, one related to overcrowding and the other to the vicissitudes of the environment, may be analogous to two phases of mortality postulated by Gulland (1965). He suggests two phases of mortality in the first few months in the life of a fish that might interact to determine its year class strength; 1) a density-dependent phase, and 2) a critical phase. The first has mortality that is higher for year classes with an initially high number of eggs than one with an initially low number of eggs. The second is one in which the strength of a given year class is determined.

Assuming Gulland's (1965) phases apply to larvae in the Sheepscot River estuary, the density-dependent phase, indicated by peaks in larval abundance, occurred in winter as well as in autumn for year classes 1974-1976 and 1978. The critical phase was established briefly in the estuary in 1974 (Fig. 6), when a peak occurred in late December, and in 1975 (Fig. 7), when a peak occurred in January, and perhaps hardly at all in 1976 (Fig. 8), when the peak occurred in February. During the winters of 1974-1976 and 1978 the occurrence of the critical phase perhaps was shortened by late spawning. Figures 6, 7 and 10 suggested that larvae forming peaks in abundance during December and January were approximately the same size as those present in October and November during 1974-1975, and 1978. Perhaps spawning occurred late during these years. Previously, hatching occurred mainly in September and October, but small hatchings also were recorded in early November during 1971-1972 (Graham et al., 1972b and 1973) and some spawning was considered possible as late as December in the 1960's (Boyar, 1968). Examination of larval otoliths in 1978 indicated that larvae within the estuary during January and February were hatched later than those occurring there in November (Townsend and Graham, MS). Larvae from the November peak in catch rate hatched about the second week in October; those from the small January peak hatched about the third week in November (Fig. 10). An increase in late spawning could account for the additional larvae found in the estuary during the winters of 1974-1975, 1978, and perhaps 1976. Such an increase could shorten the period during which the postulated critical phase existed and thus increase larval survival into the spring, when the larvae would encounter improved environmental conditions, as suggested by their higher condition factors (Chenoweth, 1970).

Larval Abundance. Possible relationships among adult herring fisheries, spawning stock and the abundance of larval herring along the Maine coast were difficult to ascertain. Although the adult fisheries on Georges Bank and in the western Gulf of Maine took large catches from 1961-1969, the stock of spawning fish was high (Anthony and Waring, 1978) and did not exhibit the general decline shown for the indices of larval abundance for the 1964-1969 year classes (Fig. 12). The low winter indices of larval abundance for year classes 1970-1973 did coincide with large reductions in the spawning stock. However, stock estimates after 1971 were uncertain (Anthony and Waring, 1978). Because the fisheries concentrated on spawning fish it was considered possible that the act of fishing disrupted spawning activities, either reducing the number of eggs deposited or hatched independent of stock size. Thus, the state of Maine included spawning closures within their management plans (Anonymous, 1978) and Anthony and Waring (1978) suggested that disrupted spawning activities might have led in part to the decline of the Georges Bank stock.

Possibly, fishing on Georges Bank and on offshore shoal areas in the western Gulf of Maine led to a reduction in the larval contribution to the Maine coast from offshore. The evidence for such a contribution through larval movement across the deeper Gulf waters was reviewed by Graham et al. (1972a), Boyar et al. (1973), and Anthony and Waring (1978). Little direct evidence, such as distribution of larvae across the Gulf, was sought by investigators. However, Messieh et al. (1971) captured small numbers of larvae distributed from Georges Bank to about 28 km off the eastern coast of Maine (Fig. 2) during February 1967 and April 1969 and April 1970. Within the same area, Davis and Norris (1976) showed larval herring distributed from Georges Bank to about 55 km off the coast during May 1976. Davis and Norris reoccupied certain of their sampling transects on the bank and captured but a few herring where they had made large catches on a cruise about three weeks earlier. They accounted for this difference in catch by suggesting a migration off the bank.

Determinants of Larval Year Class Strength. I have already suggested (Graham et al, 1972a) that larval mortality in the autumn might not reduce larval abundance to approximately the same level along the coast by early winter of each year. Some support for this suggestion is possible if the autumnal mortality (Fig. 11) stems from overcrowding.

Larval herring occur in estuaries or embayments in aggregations. Sometimes more than one aggregation is present, as in the Sheepscot River estuary (Graham, 1972a). Since the estuary appears to have a carrying capacity for larvae in early winter that is low, an additional aggregation or its equivalent is lost through mortality. Possibly, the considerable decline in catch rate of about 75 larvae per 100 m^3 in only 20 days is an example of such loss (Figures 9 and 11). Under such circumstances the dispersal of many aggregations over a large number of embayments and estuaries along the coast serves perhaps to increase the standing crop of larvae in early winter; concentration of many aggregations within a small area of coast tends to decrease the crop. The coast of Maine is very complex and the size and number of estuaries and embayments differ from place to place; apparently suitable spawning sites are available throughout its length (Fig. 15). Perhaps, by the 1970's the development of the fishery for adult herring in the Gulf of Maine altered the composition of the herring populations to the extent that if homing to specific sites occurred it was no longer precise. Shifts in the locations of egg beds along the coast would change the survival of the larvae depending upon the associated change in the availability of nursery grounds. Also, the concentration of larvae within different inshore areas from year to year would preclude adequate sampling and a consistent relationshio between any single larval index and recruitment to the sardine fishery.

If winter is a critical period for larval year class strength along the Maine coast, it may also be critical for other areas of the Gulf of Maine. Seasonal changes in larval abundance in Maine waters are similar to those off southwest Nova Scotia.(Das, 1968) and on Georges Bank (Boyar et al., 1971). Yearly changes in oceanic conditions along the coast and in the offshore Gulf of Maine are also related (Colton, 1968). Essentially, the environment throughout the Gulf of Maine is relatively similar during winter since it is influenced regionally by the weather. Assuming that the relative strength of a larval year class continues into the juvenile stage, a winter critical period that inflicts similar rates of larval mortality throughout the Gulf of Maine perhaps explains why the catch in the juvenile fishery of Maine is applicable for data of the 1960's (Anthony and Waring, 1978) as an index of recruitment to the adult fishery of Georges Bank. Indeed, a similarity in winter larval mortality in a given year throughout the Gulf in the 1960's is perhaps the common cause suggested by Anthony and Waring (1978) as being responsible for good and bad year classes unrelated to the size of any one spawning stock in the northwest Atlantic.

The effects of winter as a critical period may be circumvented partially by a relatively late larval movement into the estuaries and embayments through late spawning, as in the 1970's. The length of the critical phase in mortality may be shortened. Perhaps the increased juvenile catch during 1974-1976 reflects such a decrease (Fig. 12).

The apparent absence of a late movement into the estuary in 1977 and the large production of larval and juvenile herring of the 1977 year class does not fit the concept that a reduced population of young spawning adults was responsible for the large recruitment (Fig. 12) to the sardine fishery in 1979. However, a large catch (3,000 MT) of the 1970 year class within the coastal adult fishery of 1978 suggested that these fish at 8 years of age were still abundant along the coast. Such older and larger fish would carry about 3 times as many eggs as the younger fish at 4 to 5 years of age. A successful spawning of the 1970 year class in 1977 perhaps was responsible for the enormous number of larvae of the 1977 year class during autumn (Figs. 9 and 12). The agreement between the winter mortality of the larvae with the estimate of spring abundance in the central sampling system (Fig. 3) and the lack of agreement between the estimate of early winter abundance and the juvenile catch of the 1977 year class (Fig. 12) suggests that the larvae moved shoreward into many estuaries and embayments in the autumn of 1977 that were not sampled. Thus, our estimates probably were not representative of the entire coastal population of larvae.

Conceptual Model of Larval Production. Figure 16 depicts a model of the progression of larval abundance in a given estuary or embayment during autumn and winter. The model is based on the conceptions that; 1) the basic determinants of larval year class strength are the level of larval abundance following a density-dependent phase of mortality in autumn and a density-independent phase of mortality during winter, and 2) these basic determinants may be modified by late spawning and the shifting of spawning sites by the adult herring.

Portions of the curves of catch rate were fitted mathematically and others by eye. To approximate the decline in autumnal catch rates from larval aggregations, observed rates were plotted for the period from October to early December, 1967-69 and 1975-76 (Fig. 17). Data for these years included 4 or more overnight sets of buoyed and anchored nets during this period. Each autumnal peak in catch rate was plotted at zero days and the preceding and subsequent rates were plotted at their intervals from the peak in days. A common regression line was constructed to produce a smoothed average decline in catch rate from the autumnal peak to the early winter rate. This decline was incorporated into the curve of catch rates for larval aggregations of the autumn. The smoothed decline of the late winter aggregation was calculated from a regression of catch rates obtained during February, 1976 (Fig. 11). The moderate decline in catch rates from December through March was based on the average mortality estimated for larvae during the winter (Table 2). In addition to the catch per 100 m^3 of water strained, a rough estimate of the relative number of larvae was provided for the model in Figure 16 by multiplying the catch rate times an estimate of the volume of water (55,000,000 m^3) within the sampling area of the Sheepscot River estuary (Fig. 1).

The model is useful in illustrating events which perhaps lead to the final year class strength of larvae in the spring just prior to their change into juvenile form. In the model, larval aggregations enter a portion of an estuary (or embayment) in autumn. They are retained there and reach their peak in abundance around late October. Overcrowding of the larvae results in a severe decline in abundance very likely caused by starvation. Mortality probably exceeds the rate of decline since larvae are added to the estuary as late as early December. By this time the aggregations are disrupted either through thinning by mortality or by dispersal of the larvae. The winter mortality is presumably density-independent and much less severe than in autumn. In the model, the catch rate of 1.5/100 m^3 is reduced to .3/100 m^3 by early March; about 160,000 larvae remain in the estuary. If late spawning occurs, aggregations enter the estuary as late as February when they cause an additional peak in abundance. As in autumn the peak is followed by a severe density-dependent mortality; but, a major density-independent phase of mortality is precluded by the onset of spring. The larval abundance is at 650,000 larvae, about 4 times that in the absence of late spawning. If winter aggregations enter in late December or January, a density-independent phase of mortality occurs. To increase the spring production beyond that possible with just autumn aggregations it is suggested that the abundance at the beginning of the density-independent phase exceeds that which would be present in the absence of winter aggregations. That is, during the density-independent phase of mortality which begins in early December the population might be reduced below the carrying capacity of the estuary, in relation to forage. With a continuation of the initial winter rate of death, the larval abundance at the beginning of spring would be between 160,000 - 650,000 larvae. Under such circumstances, the later the entrance of winter aggregations into the estuary the greater their contribution to spring abundance.

The single autumnal aggregation depicted in the model is intended to represent its entrance into the estuary with coincident distribution of residual aggregations to other estuaries or embayments otherwise unoccupied by larvae. For example, if two aggregations were involved in such a distribution under similar environmental circumstances, the initial spring abundance would be doubled, 320,000 rather than 160,000 larvae.

This model does not consider all larvae hatched along the coast. Some do not enter the estuaries and embayments until spring. A comparison of inshore and coastal catch rates in autumn and winter by Graham et al. (1972a) suggests that most larvae enter inshore water. But, data in Table 3 indicate that the percentage of larvae inshore would be difficult to estimate unless inshore waters are thoroughly sampled and larvae originate only from coastal spawnings, not from offshore. Comparisons of the mortalities of larvae that overwinter in coastal water and those that move inshore are difficult to obtain. If, after yolk sac absorption and successful initial feeding, the coastal larvae suffer a mortality that is density-dependent, then that mortality may be very high since they occur in large "patches" (Graham et al., 1973). The relatively good condition of the larvae upon entering the Sheepscot River estuary (Fig. 11) may reflect the successful dispersion of these larvae shoreward rather than the circumstances of larval patches within the coastal water. Studies in offshore waters presently pursued, may reveal mortalities within large larval patches (Lough, 1979).

Recruitment to the Coastal Fishery. Because this investigation coincided with rapidly changing fish stocks and fisheries, it was difficult to link positively, over several years, the mechanisms leading to the production of larvae with the harvest of the sardine herring. However, this linkage was indicated by the agreement of the annual harvest with the early winter larval catch rate (Fig. 14), perhaps the spring catch rate of the 1960's (Fig. 13), late spawning (1974-1976) and the large catch rate during the autumn of 1977 (Fig. 12). Assuming that a linkage exists permits some interpretation of past harvests and the possibilities of those in the future. The large decline in sardine harvests during the 1960's did not coincide with any development of a large fishery (Anthony, 1972). Possibly, the large mortalities (>80%) during the winter critical period of the larvae were responsible for this decline. In the early 1970's the development of the adult fishery in the Gulf of Maine peaked and probably stressed the coastal stocks. Under such stress, the coastal herring was reasonably productive while similar stress upon the fishery on Georges Bank caused it to collapse (Anthony and Waring, 1978). It is suggested that the recruitment mechanism primarily responsible for the success of the coastal herring under stress has been the opportunity of its larvae to distribute themselves inshore utilizing these waters efficiently as nursery grounds. Careful management of these inshore nursery grounds might favor a continuing fishery, even when management fails to remove stress upon the coastal stocks.

ACKNOWLEDGEMENTS

The larval research in this paper began in 1962 under the auspices of the U.S. Bureau of Commercial Fisheries of the Department of Interior, continued under the U.S. National Marine Fisheries Service of the Department of Commerce, and is presently pursued under the Maine Department of Marine Resources. Over this period a number of scientists and technicians assisted in the collection of data: Ronald Aho, Chris Adams, Bruce Bickford, Stanley Chenoweth, Clarence Davis, Paul Venno and George Vaughn.

I am grateful to Vaughn Anthony, Jean Chenoweth and Lewis Lozier, who supplied data on juvenile herring for comparison with those of larval herring. Marie Willard of St. Francis College and Susan Driscoll of Bates College assisted in studies of larval condition.

LITERATURE CITED

Anonymous. 1978. Herring regulations. Maine Dept. Mar. Resources.

Anthony, V.C. 1972. Population dynamics of the Atlantic herring in the Gulf of Maine. Ph.D. thesis, Univ. of Wash., Seattle, Wash. 266p.

Anthony, V.C. and G. Waring. 1978. Assessment and management of the Georges Bank herring fishery. Symposium on the biological basis of pelagic fish stock management. Int. Explor. Mer., No. 4: 74p.

Boyar, H.C. 1968. Age, length, and gonadal stages of herring from Georges Bank and the Gulf of Maine. Int. Comm. Northw. Atlant. Res. Bull. 5:49-61.

Boyar, H.C., R.R. Marak, F.E. Perkins and R.A. Clifford. 1973. Seasonal distribution and growth of larval herring (*Clupea harengus*) L.) in the Georges Bank-Gulf of Maine area from 1962 to 1970. J. Cons. 35(1):36-51.

Chenoweth, S.B. 1970. Seasonal variations in condition of larval herring in Boothbay area of the Maine coast. J. Fish. Res. Bd. Can. 27(10):1875-1879.

Colton, J.B., Jr. 1968. Recent trends in subsurface temperatures in the Gulf of Maine and contiguous waters. J. Fish. Res. Bd. Can. 25:2427-2437.

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

Davis, C.W. and T.L. Norris. 1976. Preliminary report on the distribution, catches and sizes of age 1 herring in the Gulf of Maine, Georges Bank and Nantucket Shoals during spring of 1976. Int. Comm. Northw. Atlant. Fish. Res. Doc. 76/VI/114:80p.

Dow, R.L. 1976. Effects of climatic cycles on the relative abundance and availability of commercial marine and estuarine species. J. Cons. Int. Explor. Mer., 37(3):274-280.

Graham, J.J. 1980a. The effects of length of tow upon the catch of larval herring, *Clupea harengus*, in coastal Maine. Maine Dept. Mar. Resour., Res. Ref. Doc. 80/4:10p.

Graham, J.J. 1980b. An experiment on the depth distribution of large larval herring, *Clupea harengus*, in coastal Maine. Maine Dept. Mar. Resour., Res. Ref. Doc. 80/1:15p.

Graham, J.J. 1972a. Retention of larval herring within the Sheepscot estuary of Maine. Fish. Bull., U.S. 70(2):299-305.

Graham, J.J. 1972b. Filtration efficiencies of Boothbay Depressor nets. Fish. Bull., U.S. 70:518-520.

Graham, J.J. 1970a. Coastal currents of the western Gulf of Maine. Int. Comm. Northwest Atl. Fish. Res. Bull. 7:19-31.

Graham, J.J. 1970b. Temperature, salinity and transparency observations, coastal Gulf of Maine, 1962-65. U.S. Fish. Wildl. Serv., Data Rep. 42, 43p.

Graham, J.J. and C.W. Davis. 1971. Estimates of mortality and year class strength of larval herring in western Maine, 1964-67. Cons. Perm. Int. Explor. Mer., Rapp. P.-v. Reun. 160:147-152.

Graham, J.J. and P.M.W. Venno. 1968. Sampling larval herring from tidewaters with buoyed and anchored nets. J. Fish. Res. Bd. Can. 25:1169-1179.

Graham, J.J. and G.B. Vaughn. 1966. A new depressor design. Limnol. Oceanogr. 11:130-135.

Graham, J.J., S.B. Chenoweth and C.W. Davis. 1972a. Abundance, distribution, movements and lengths of larval herring along the western coast of the Gulf of Maine. Fish. Bull., U.S. 70:307-321.

Graham, J.J., C.W. Davis, S.B. Chenoweth and B.C. Bickford. 1972b. Autumnal distribution, abundance and dispersion of larval herring, *Clupea harengus harengus* Linnaeus, along the western coast of the Gulf of Maine in 1971. Int. Comm. Northw. Atlant. Fish. Res. Doc. 72/7:11p.

Graham, J.J., C.W. Davis and B.C. Bickford. 1973. Autumnal distribution, abundance and dispersion of larval herring, *Clupea harengus harengus* Linnaeus, along the western coast of the gulf of Maine. Int. Comm. Northw. Atlant. Fish. Res. Doc. 73/12:32p.

Gulland, J.A. 1965. Survival of the youngest stages of fish, and its relation to year class strength. Int. Comm. Northw. Atlant. Fish. Spec. Publ. 6:363-371.

LeCren, E.D. 1951. The length-weight relationship and seasonal cycle in gonad weight and condition in perch (*Perca Fluviatilis*). J. Anim. Ecol. 20:201-219.

Lough, R.G. 1979. Larval herring patch study. Int. Comm. Northw. Atlant. Fish. Res. Doc. 79/VI/116: 3 p.

Messieh, S.N., S.N. Tibbo and L.M. Lauzier. 1971. Distribution, abundance, and growth of larval herring (*Clupea harengus* L.) in Bay of Fundy-Gulf of Maine area. Fish. Res. Bd. Can. Tech. Rep. 277, 18p.

Sherman, K. and K.A. Honey. 1970. Seasonal variations in the food of larval herring in coastal waters of central Maine. Cons. Perm. Int. Explor. Mer., Rapp. P.-v. Reun. 160:121-124.

Townsend, D.W. and J.J. Graham. MS. Growth and age structure of larval herring (*Clupea harengus* L.) in the Sheepscot River estuary of Maine as determined by daily growth increments in otoliths. 22p.

Table 1. Catch data from buoyed and anchored nets set in the Sheepscot River estuary during winter for larval year classes 1964-1973 and 1977.

Year Class	Sampling Date	Larvae Caught Number	Larvae Caught Number/100 m^3	Sampling Date	Larvae Caught Number	Larvae Caught Number/100 m^3
1964	16 Dec.	1849	5.59	30 Dec.	287	3.33
1965	9 Dec.	928	2.96	20 Jan.	252	1.45
1966	21 Dec.	1045	5.46	20 Jan.	826	3.99
1967	18 Dec.	462	2.06	18 Jan.	197	1.03
1968	12 Dec.	736	4.08	7 Jan.	468	2.35
1969	15 Dec.	96	0.58	15 Jan.	38	0.21
1970	21 Dec.	232	1.95	18 Jan.	149	0.95
1971	16 Dec.	157	0.47	13 Jan.	134	0.42
1972	22 Dec.	146	0.49	21 Jan.	116	0.32
1973	23 Dec.	174	1.31	18 Jan.	104	0.40
1977	21 Dec.	774	1.39	15 Jan.	117	0.25

Table 2. Estimates of instantaneous winter mortality for larval herring, year classes 1964-1973 and 1977.

Year Class	Mortality Over Sampling Period (zt)	Number of Tidal 1/ Phases (t)	Mortality per Tidal Phase (z)	Winter Mortality Rate 2/ (372z)	Percent Mortality Winter Period
1964	.515	56	.00920	3.42	96.7
1965	.715	161	.00444	1.65	80.8
1966	.313	76	.00412	1.53	78.4
1967	.693	122	.00568	2.11	87.9
1968	.551	99	.00556	2.07	87.4
1969	1.016	117	.00868	3.23	96.0
1970	.719	106	.00678	2.52	92.0
1971	.112	106	.00106	0.39	32.3
1972	.426	106	.00402	1.50	77.5
1973	.486	98	.00495	1.84	84.1
1977	.726	108	.00672	2.50	91.8

1/ Semidiurnal tidal phase (6 hr.+)

2/ Unit time period: 3 mos.

Table 3. Spring larval catch rates, indices of larval abundance for coastal and inshore areas and estimates of relative abundance (combined).

Year Class	Sampling Period	Number of Larvae Coastal	Inshore	Combined	Catch per 100 m^3 Coastal	Inshore	Combined
(I) Central sampling system.							
1965	9-22 Mar. 1966	603	68	671	1.00	0.41	1.41
1966	28 Mar.-6 Apr. 1967	284	136	420	0.49	0.90	1.39
1967	3-12 Apr. 1968	120	193	313	0.22	1.05	1.27
1968	15-22 Apr. 1969	160	208	368	0.31	0.99	1.26
1969	7-13 Apr. 1970	94	77	171	0.17	0.56	0.73
1970	30 Mar.-12 Apr. 1971	90	258	348	0.20	1.15	1.40
1971	30 Mar.-12 Apr. 1972	33	482	515	0.04	1.57	1.61
1972	16-22 Apr. 1973	328	130	458	0.84	0.50	1.34
1973	11-26 Apr. 1974	120	171	291	0.32	0.66	0.98
1974	10-16 Apr. 1975	17	362	379	0.04	1.20	1.24
1975	7-13 Apr. 1976	77	110	187	0.20	0.47	0.67
1976	11-19 Apr. 1977	107	1169	1176	0.28	3.01	3.29
1977	29 Mar.-10 Apr. 1978	33	159	192	0.08	0.68	0.94
1978	11-16 Apr. 1979	14	44	58	0.08	0.41	0.49
(II) Eastern sampling system							
1973	3-8 Apr. 1974	56	41	97	.13	.11	.24
1974	2-10 Apr. 1975	102	152	254	.25	.70	.95
1975	26-30 Mar. 1976	81	19	100	.24	.19	.43
1976	28 Mar.-2 Apr. 1977	39	97	136	.11	.51	.62
1977	28-30 Mar. 1978	23	23	46	.06	.15	.21
1978	27 Mar.-4 Apr. 1979	128	112	240	.43	.57	1.00
(III) Western sampling system							
1974	11-18 Apr. 1975	57	98	155	.42	.78	1.20
1975	14-15 Apr. 1976	31	33	64	.23	.20	.43
1976	19-20 Apr. 1977	60	155	215	.32	.82	1.14
1977	10-12 Apr. 1978	32	112	144	.17	.56	.73
1978	16-19 Apr. 1979	45	48	93	.47	.59	1.06

Table 4. Average condition factor for larval herring in the Sheepscot River estuary. Length-weight regressions are calculated for data from each year class (1976 and 1977), where w is the estimated weight in logarithms and L is the standard length in logarithms.

1976–1977			1977–1978			1978–1979		
Sampling Date	Number of Larvae	Condition Factor	Sampling Date	Number of Larvae	Condition Factor	Sampling Date	Number of Larvae	Condition Factor
4 Oct.	50	1.848	6 Oct.	50	1.223	5 Oct.	6	0.805
18 Oct.	24	1.183	20 Oct.	49	1.188	19 Oct.	90	1.362
10 Nov.	42	0.979	9 Nov.	49	0.963	2 Nov.	78	0.930
29 Nov.	50	1.070	28 Nov.	50	1.157	16 Nov.	136	1.032
14 Dec.	48	0.924	8 Dec.	50	1.092	4 Dec.	84	0.857
20 Dec.	50	0.914	15 Dec.	48	1.1978	13 Dec.	47	0.846
3 Jan.	49	0.744	27 Dec.	50	0.966	21 Dec.	55	0.897
24 Jan.	49	1.028	12 Jan.	11	1.186	3 Jan.	45	1.118
7 Feb.	49	0.941	19 Jan.	50	1.128	15 Jan.	52	1.268
22 Feb.	45	0.880	25 Jan.	50	0.839	29 Jan.	61	1.103
2 Mar.	48	0.755	2 Feb.	50	1.228	8 Feb.	56	0.995
			16 Feb.	49	0.952	27 Feb.	42	1.046
			27 Feb.	50	0.838			
$\hat{w} = -9.293 \quad 4.511\ L$			$\hat{w} = -7.746 \quad 3.894\ L$			$\hat{w} = -6.4192 + 3.389L$		

Table 5. An index of anticipated abundance of the juvenile herring catch totaled for ages 1, 2 and 3. December larval data are from Table 1.

Year Class	Larvae: Dec. No./100 m3	x Survival	= Index	Juveniles Millions
1964	5.59	.033	.184	454
1965	2.96	.192	.568	441
1966	5.46	.216	1.179	1148
1967	2.04	.121	.247	269
1968	4.08	.126	.514	206
1969	0.58	.036	.021	71
1970	1.95	.080	.156	520
1971	0.47	.677	.318	208
1972	0.49	.255	.110	211
1973	1.31	.159	.208	313

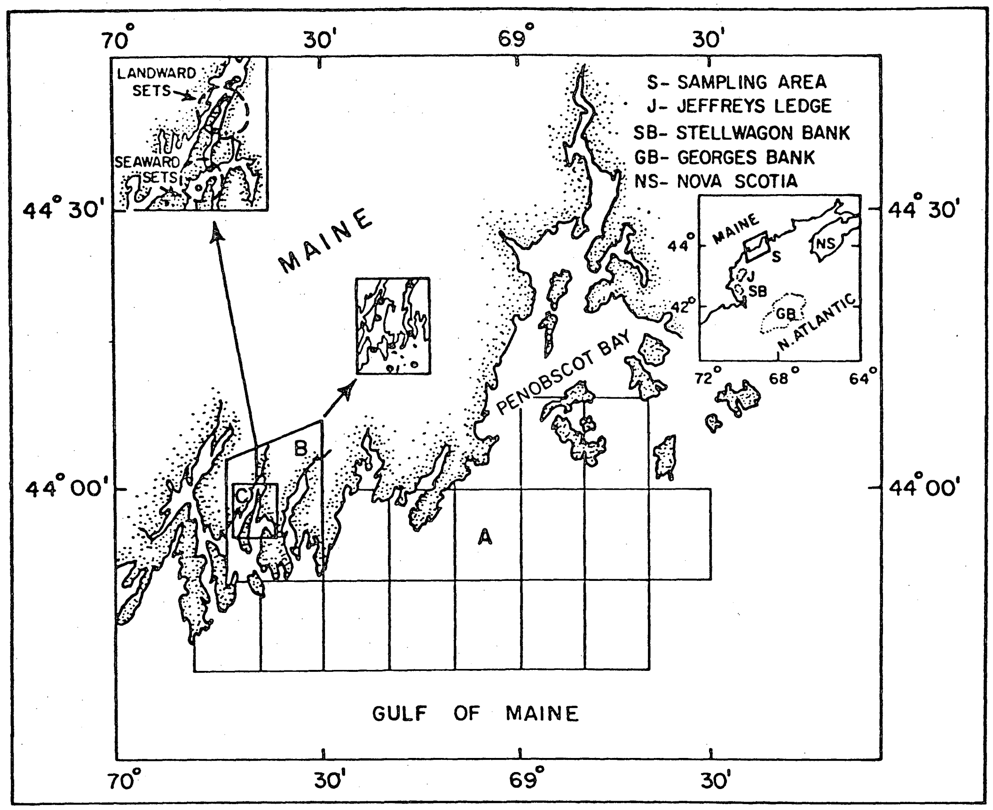

Fig. 1. Location of monitoring stations for 1964-1978. A - coastal along shore with towed gear in spring. B - inshore, with towed gear in spring. C - estuarine (Sheepscot River), with buoyed and anchored nets in autumn and winter.

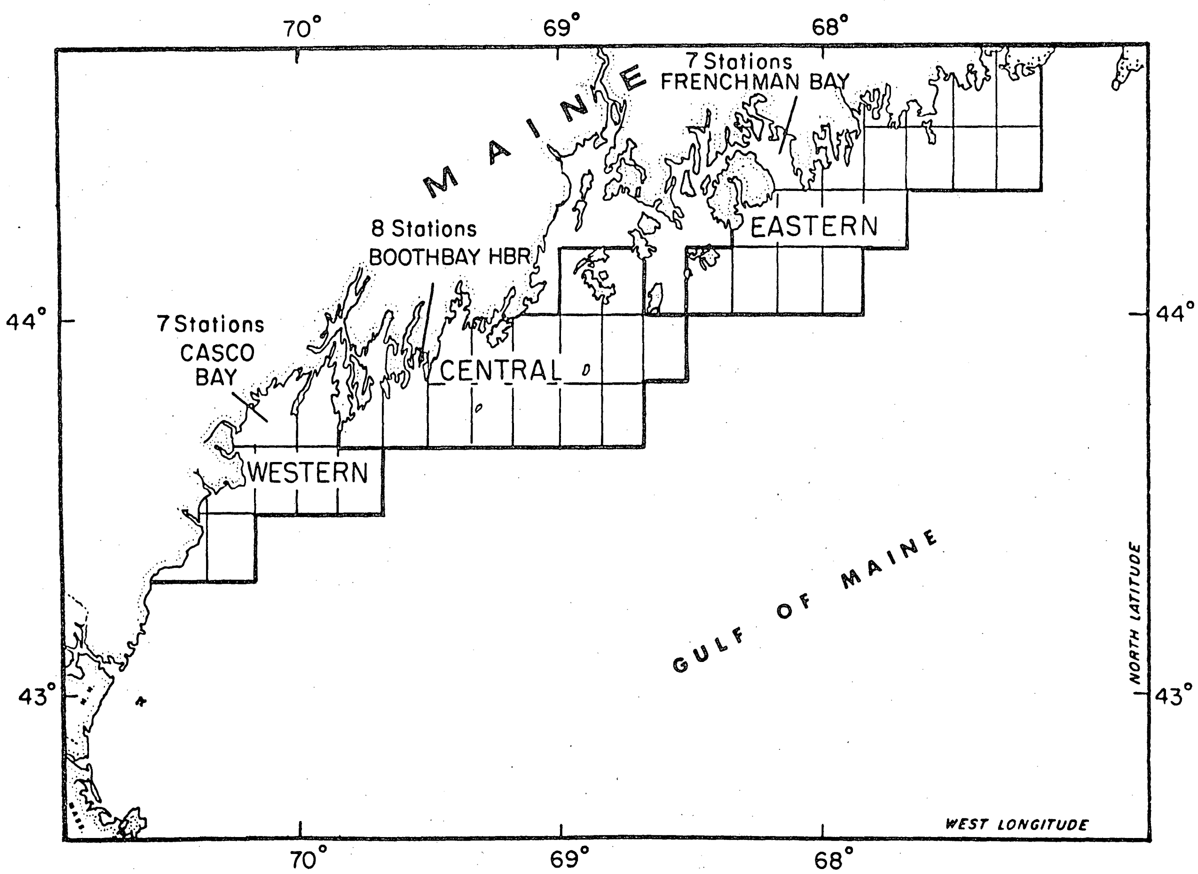

Fig. 2. Inshore and coastal sampling stations for three areas; eastern, central and western, of coastal Maine.

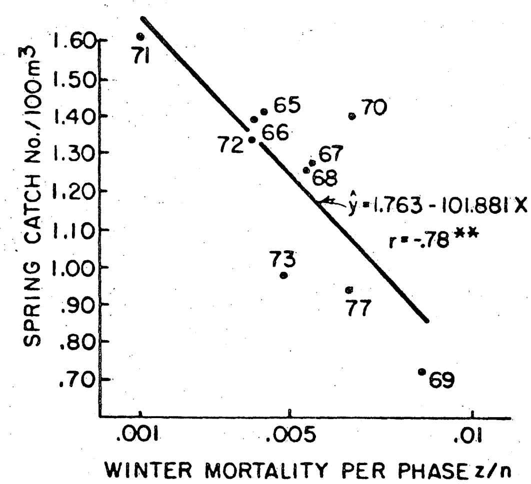

Fig. 3. Relation between estimates of winter mortality (Table 2) and the index of spring abundance (Table 3) of coastal Maine. Two asterisks indicate statistical significance of $P_{.01}$.

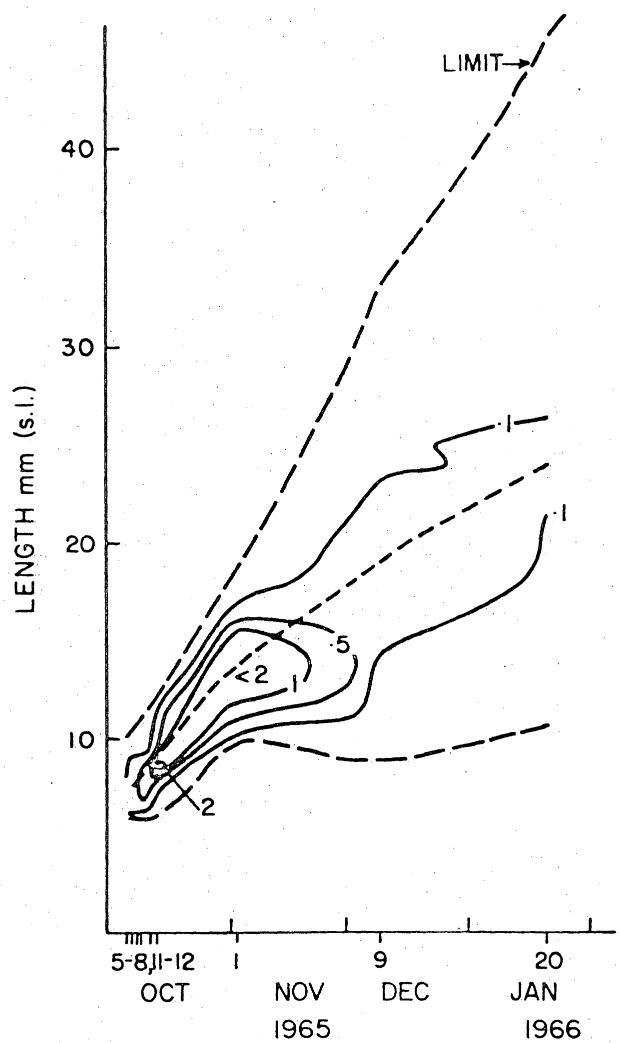

Fig. 4. Contours of catch rate (no./100m^3) by larval size for year class 1965 during autumn and winter. Mean length and the maximum and minimum size limits are indicated by dashed lines. Sampling dates are indicated on the abscissa.

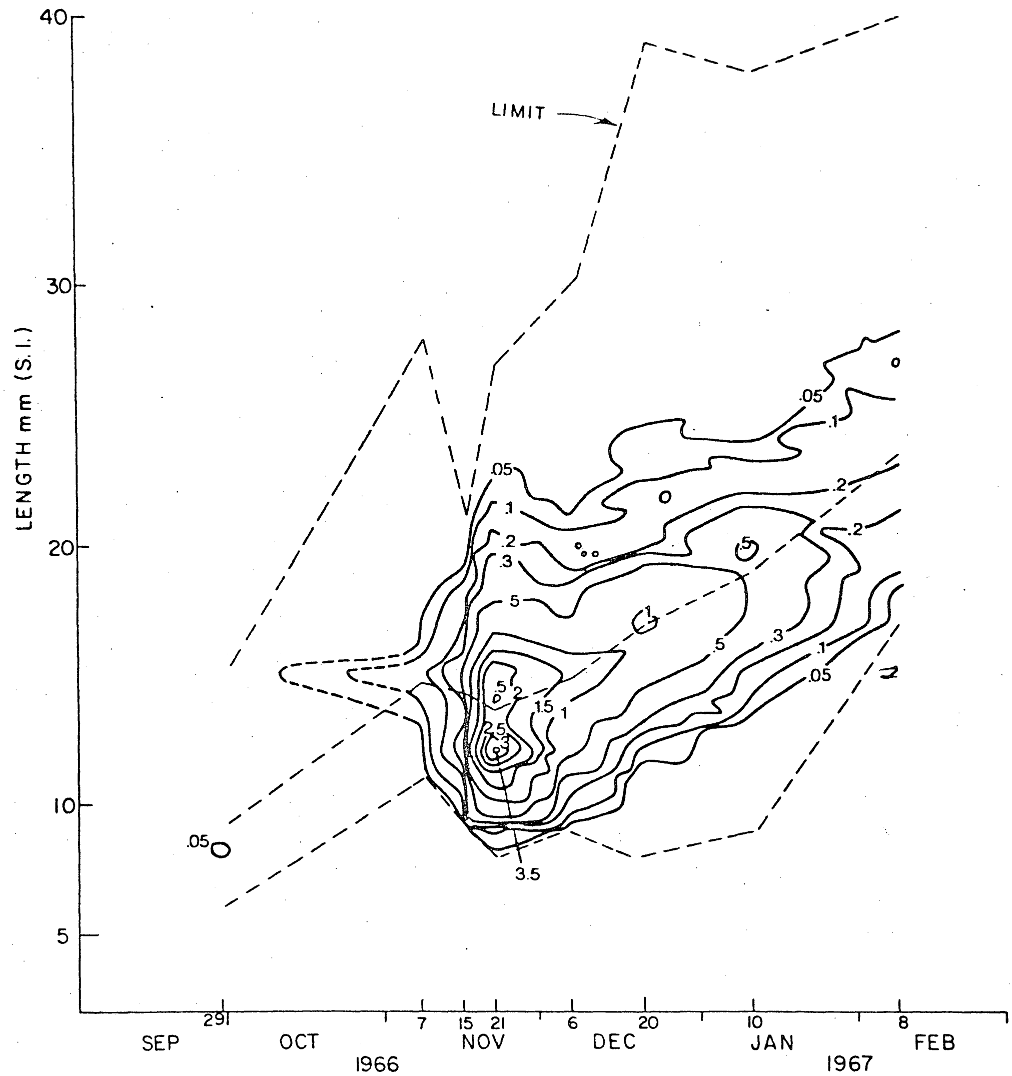

Fig. 5. Contours of catch rates (no./100 m^3) by larval size for year class 1966 during autumn and winter. Mean length and maximum and minimum size limits are indicated by dashed lines. Sampling dates are indicated on the abscissa.

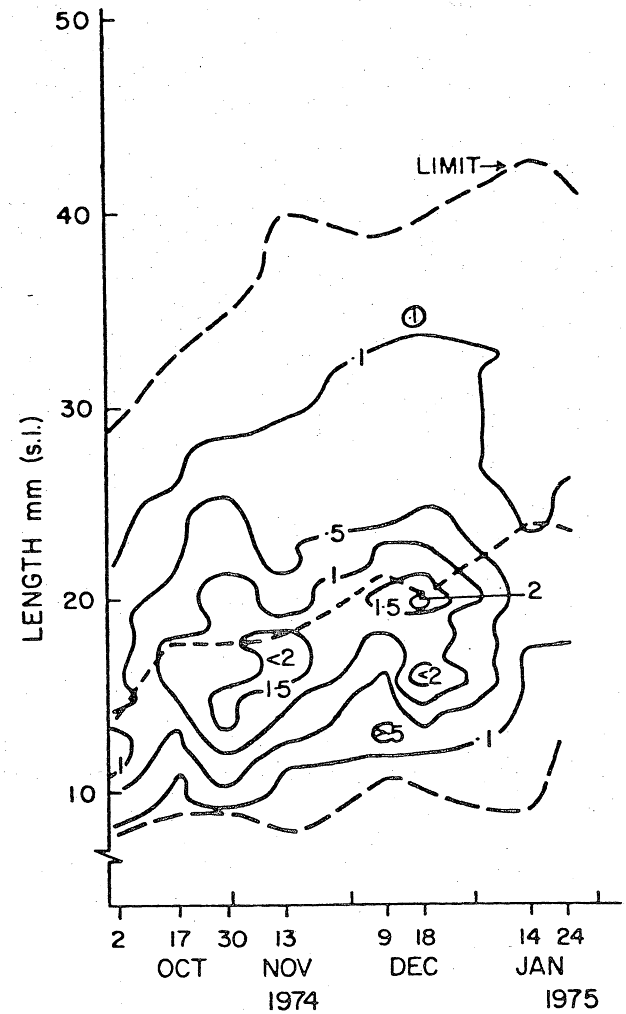

Fig. 6. Countours of catch rates (no./100 m^3) by larval size for year class 1974 during autumn and winter. Mean length and maximum and minimum size limits are indicated by dashed lines. Sampling dates are indicated on the abscissa.

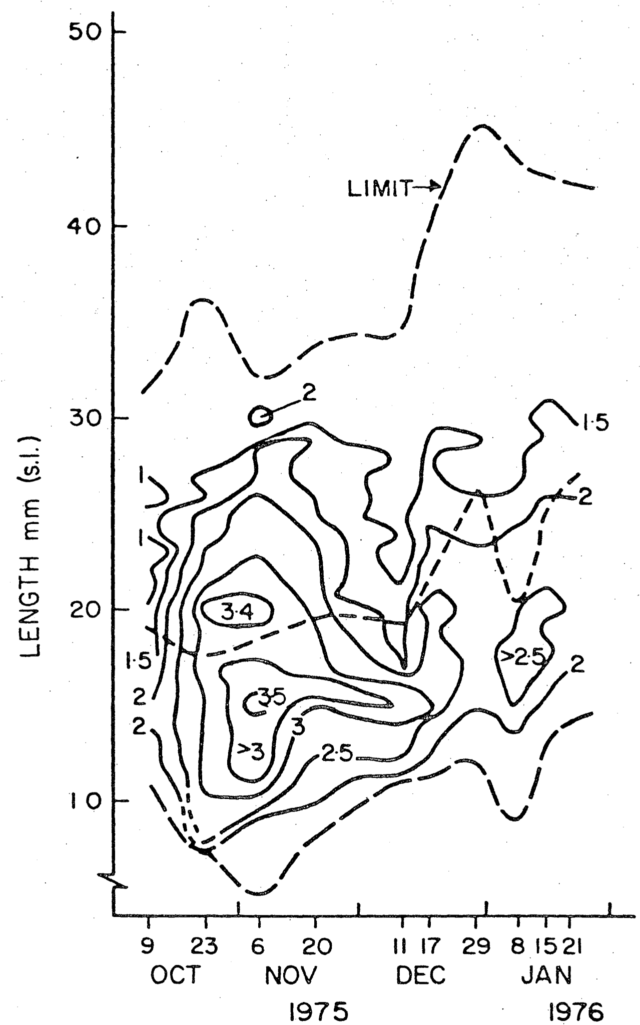

Fig. 7. Contours of catch rates (no./100 m^3) by larval size for year class 1975 during autumn and winter. Mean length and maximum and minimum size limits are indicated by dashed lines. Sampling dates are indicated on the abscissa.

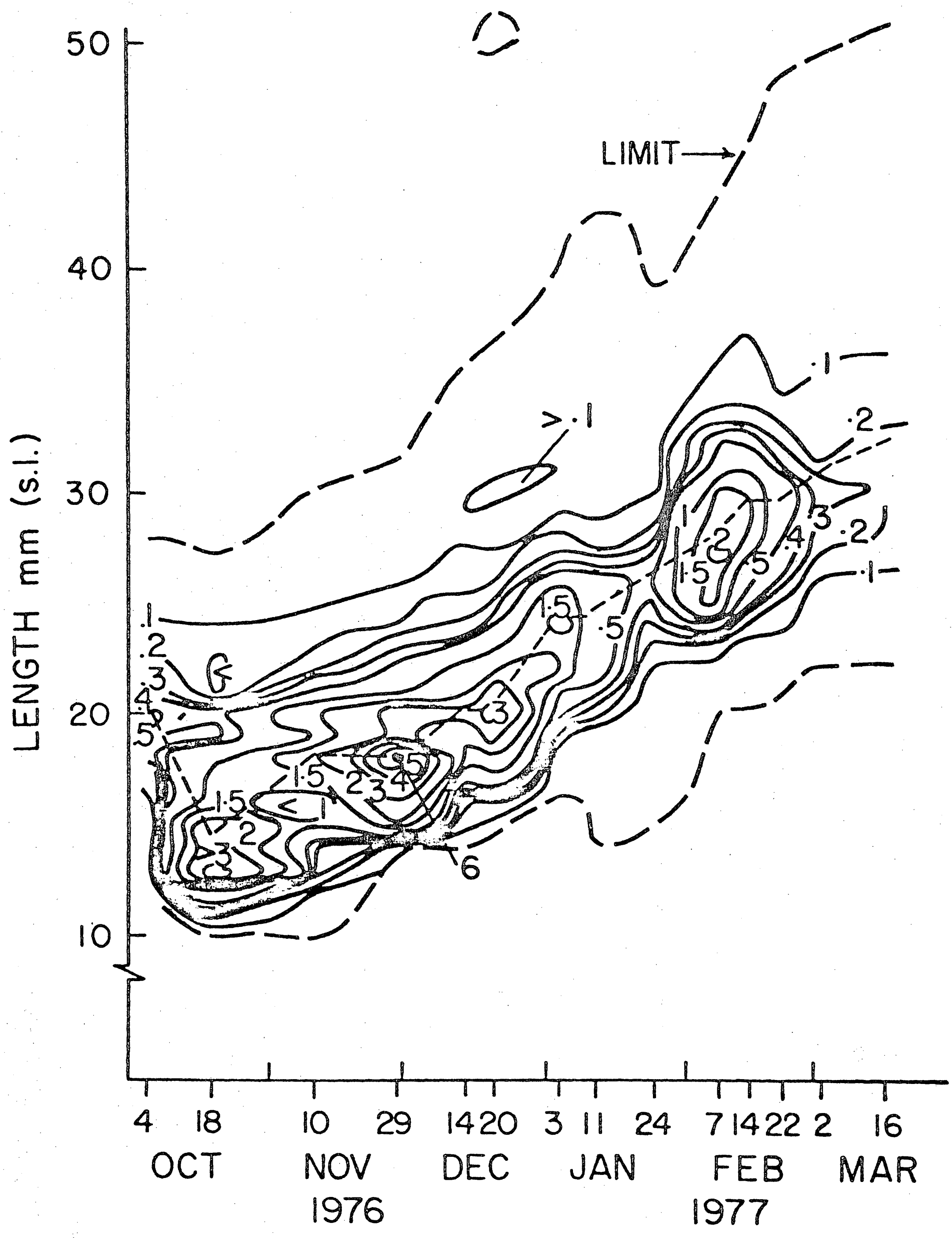

Fig. 8. Contours of catch rates (no./100 m^3) by larval size for year class 1976 during autumn and winter. Mean length and maximum and minimum size limits are indicated by dashed lines. Sampling dates are indicated on the abscissa.

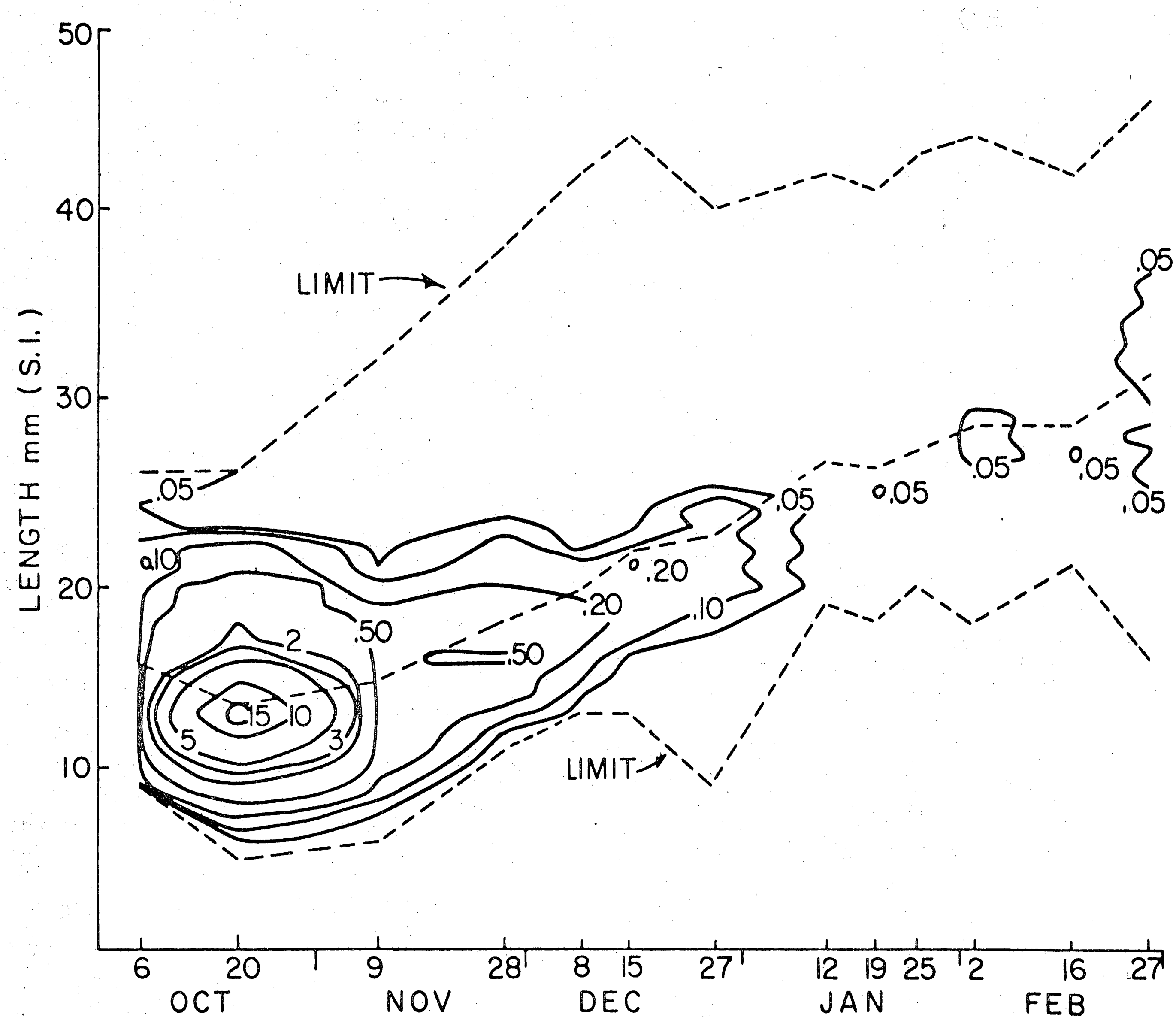

Fig. 9. Contours of catch rates (no./100 m^3) by larval size for year class 1977 during autumn and winter. Mean length and maximum and minimum size limits are indicated by abscissa.

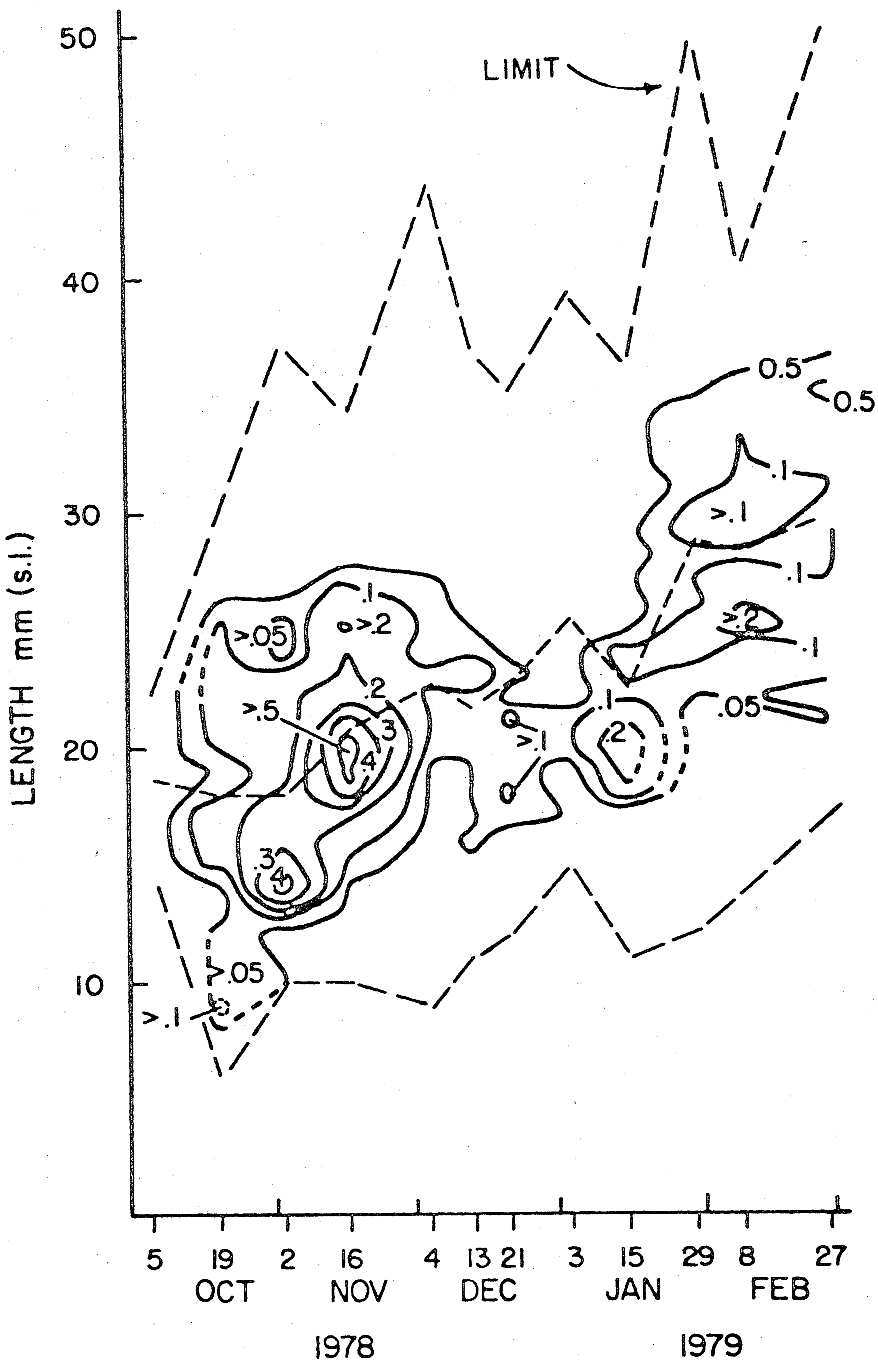

Figure 10. Contours of catch rates (no./100 m^3) by larval size for year class 1978 during autumn and winter. Mean length and maximum and minimum size limits are indicated by dashed lines. Sampling dates are indicated on the abscissa.

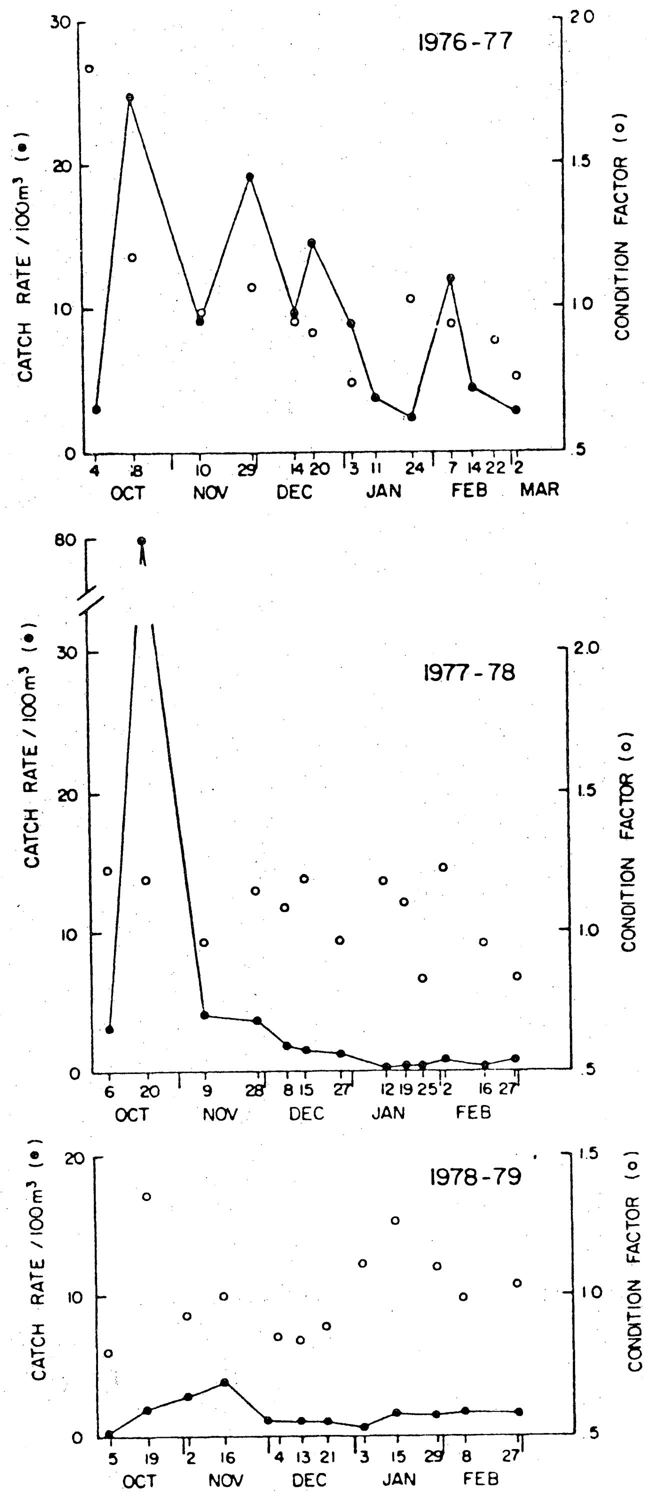

Figure 11. The variation in the condition factor and catch rate (no./100 m^3) of larval year classes 1976-78 during autumn and winter.

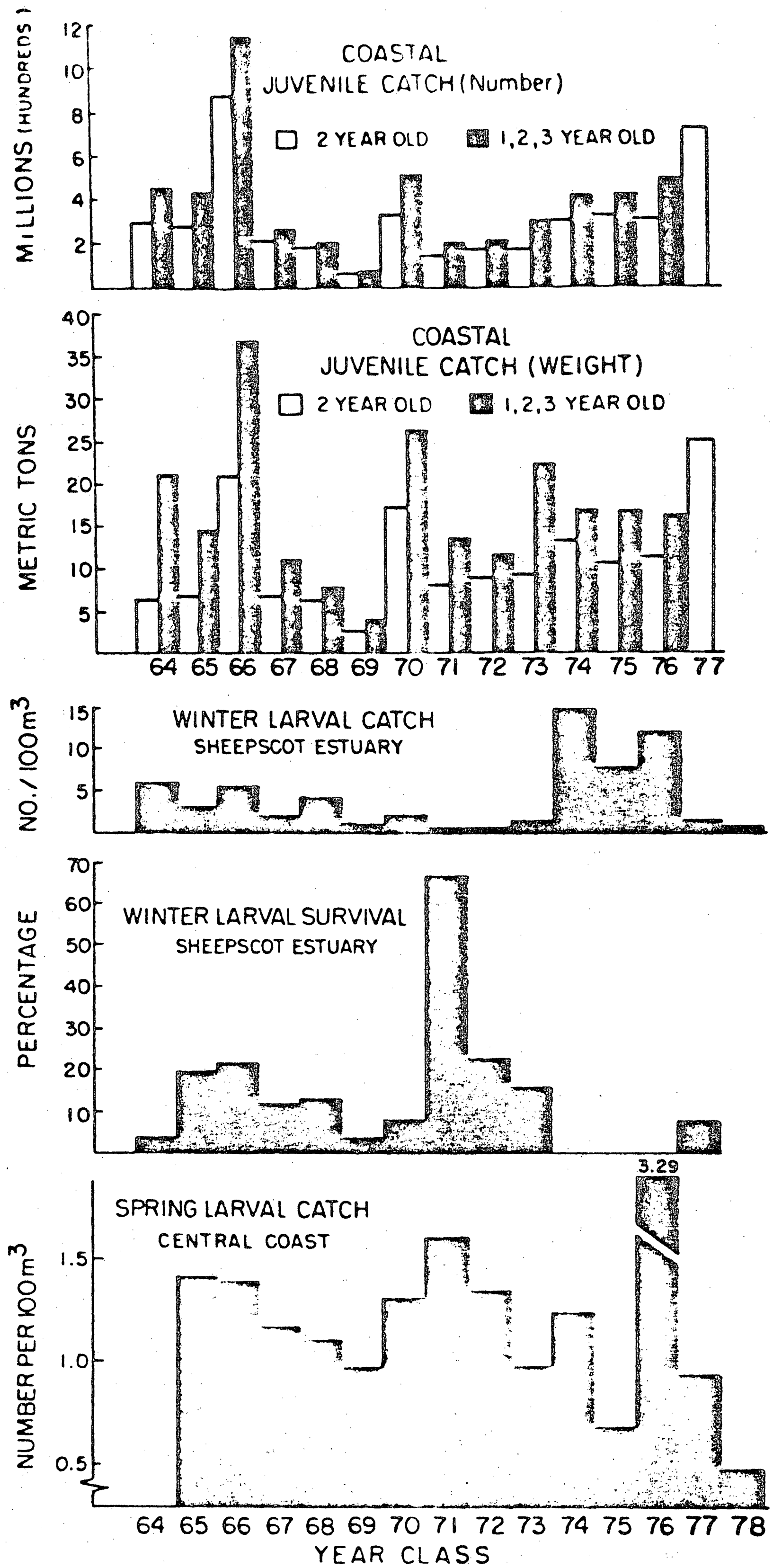

Figure 12. Comparison of larval survival, early winter and spring catch (no./100 m^3) with the number and weight of juvenile herring captured along the Maine coast.

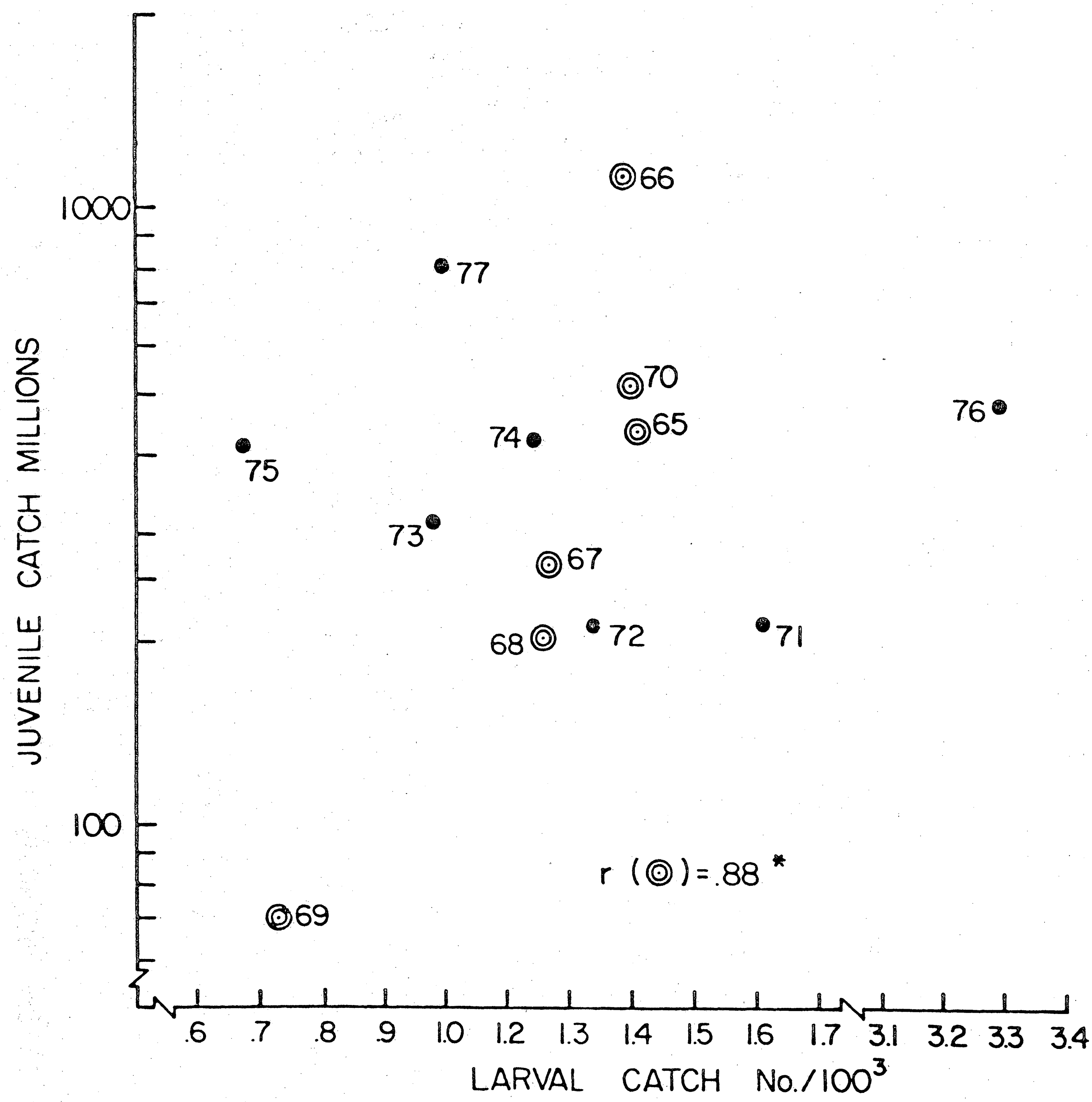

Figure 13. Relation of larval catch rates during spring to the harvest of juveniles as 1-, 2-, and 3-year old fish for year classes 1965-1977. Data for 1977 include only 1- and 2-year old fish. Year classes 1965-1970 are plotted as double zeros and the remaining as dots.

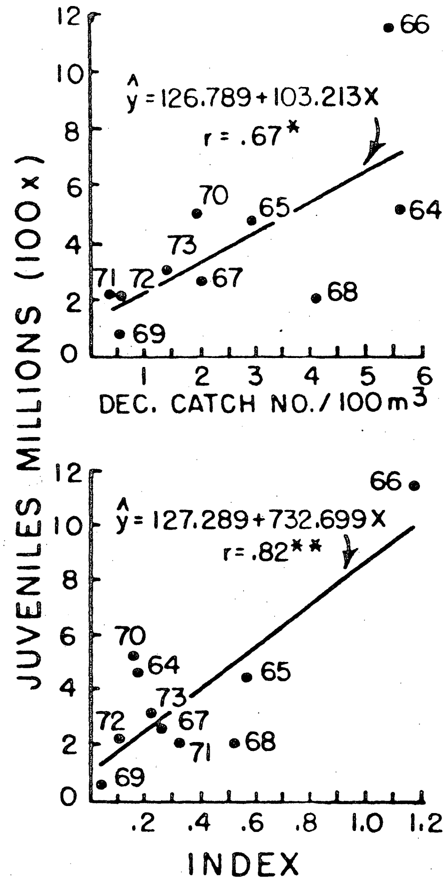

Figure 14. Relation between the coastal juvenile catch and the early December catches of larval year classes, 1964-73 (top panel); and, between an index indicating the effect of winter mortality on the initial standing larval crop (bottom panel). A single asterisk indicates statistical significance at the 5% level; a double asterisk, at the 1% level.

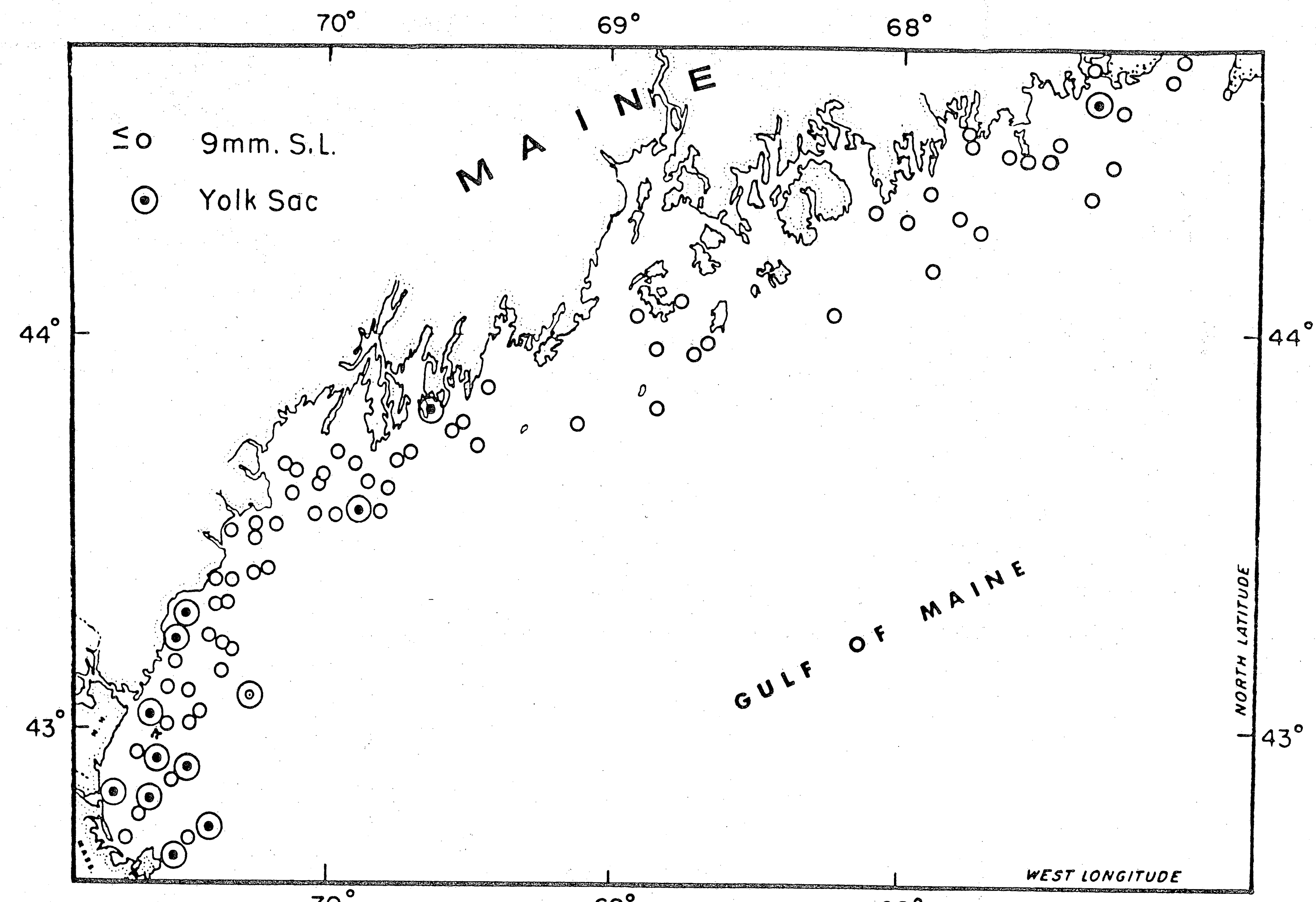

Figure 15. Locations of recently hatched larvae ($\leq$ 9 mm S.L.), some with yolk sacs, captured along the coast of Maine in the 1960s.

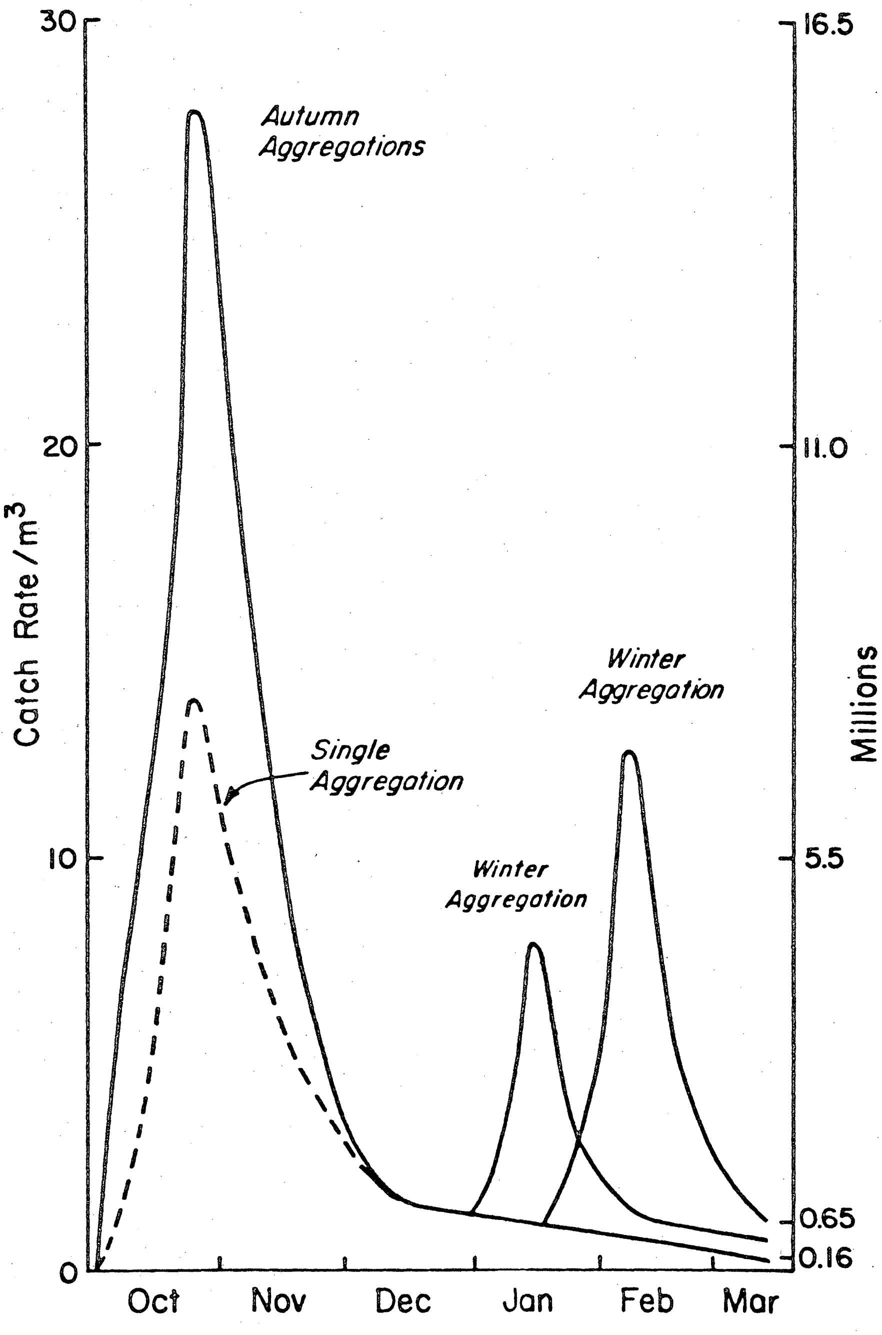

Figure 16. Conceptual model of larval production within the inshore waters of Maine.

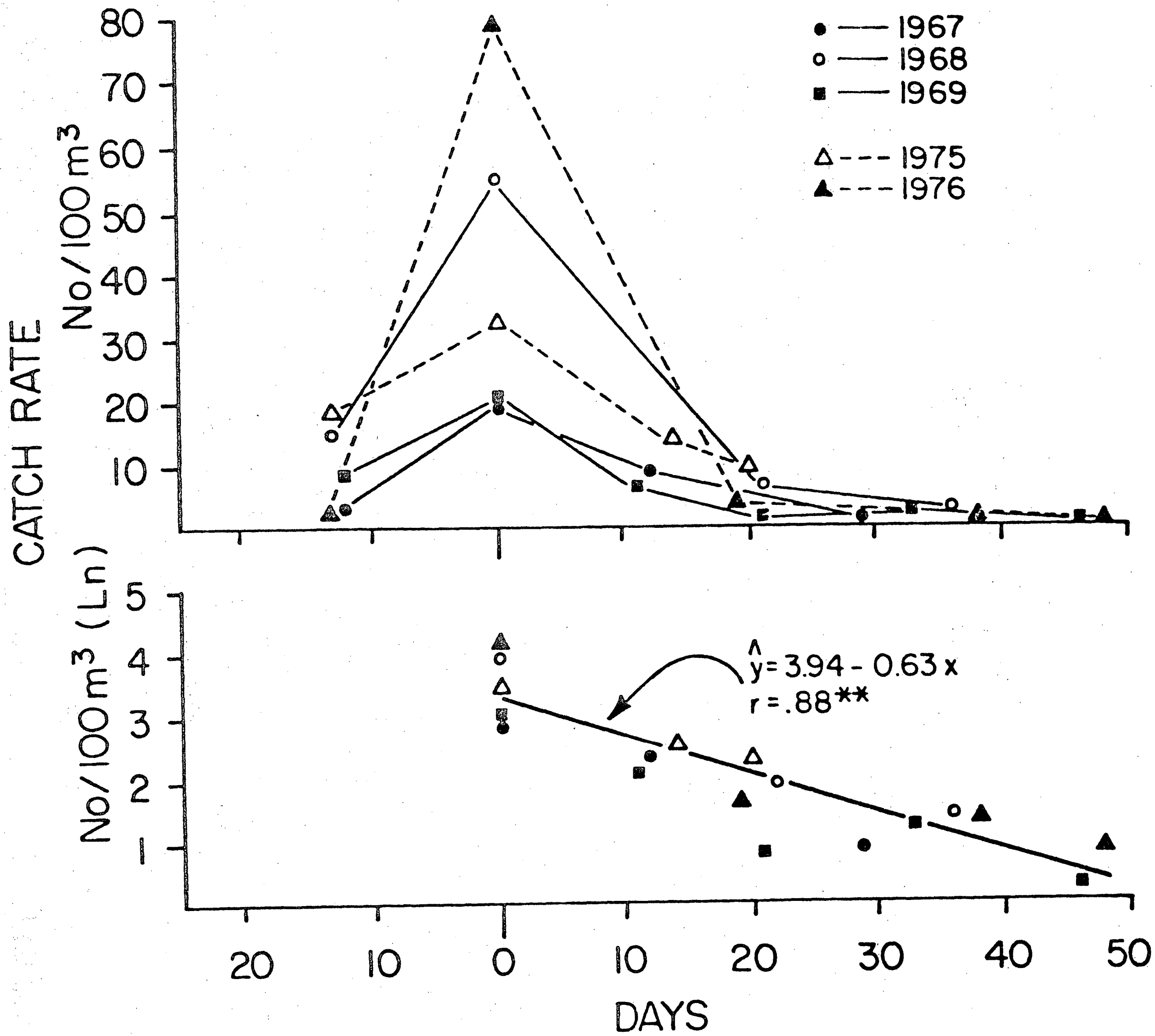

Figure 17. Observed autumnal catch rates of larval herring in the Sheepscot River estuary. Upper panel - peak catch rates are plotted at zero and others are plotted at their intervals of sampling in days from the peak catch rate. Lower panel - a common regression line for the peak and subsequent catch rates in natural logarithms.