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# Synopsis of Knowledge of the Recruitment Process for Atlantic Herring with Special Reference to Georges Bank

by

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SPECIAL SESSION ON RECRUITMENT

## INTRODUCTION

Rapid development of the large international fishery for adult herring on Georges Bank during the 1960's, and the drastic decline in abundance of the stock during the late 60's and early 70's was coincident with the development or expansion of adult herring fisheries on the other major spawning groups in the Gulf of Maine, and a concurrent decline in the harvest of the juvenile herring fisheries. These events, together with uncertainty and concern over the possible interrelationship of these stocks, led to a series of new herring research initiatives, both national and international, in an attempt to clarify the biology of herring and especially to determine the discreteness of the stocks.

The ICNAF larval herring program from 1971 to 1978 was the largest of these efforts. Initially, it was designed to delimit the principal spawning grounds of the various stocks of the Gulf of Maine region, to provide fishery independent estimates of the relative sizes of the stocks, and to document the dispersal of larvae during their first few months to contribute information on possible stock interrelationships. From the beginning, it was recognized that the larval surveys were only a partial step toward solving the stock interrelationship questions, and there was no general expectation that recruitment predictions would necessarily be forthcoming. It was noted that studies of distribution, abundance and movements of post-larvae and juvenile populations should also be intensified and that these probably would be required to clarify the stock interrelationships, and would also be more likely to provide the recruitment predictions needed for assessment and management. International juvenile herring surveys were also conducted in addition to the larval surveys in an attempt to develop recruitment indices.

The next major field program directed at herring was the international herring tagging program designed to determine the seasonal migrations and inter-mixtures of adult and juvenile stages of the principal herring stocks. Although the Georges Bank stock collapsed before definitive tagging experiments could be carried out there, results from tagging studies of the other stocks clarified general migration patterns and inter-mixing such that stronger inferences can be drawn about some aspects of the recruitment process for Georges Bank.

The purpose of this paper is to provide a very brief overview of the development and results of these and other studies on Atlantic herring, with emphasis on what knowledge has been acquired that is relevant to an understanding of the recruitment process. It is by no means a thorough review of the literature, but rather is based on recent review papers and other selected papers which deal specifically with recruitment and current hypotheses about controlling mechanisms. The Georges Bank stock has received the major focus in keeping with the original intent of this special session, but results from other stocks in the North Atlantic are also included. It is my hope that it will provide a useful background and framework for interpretation of presented papers and discussions at this special session on recruitment.

## STOCK DEFINITIONS AND MOVEMENTS OF HERRING IN GULF OF MAINE REGION

Three major herring stocks have been identified in the Georges Bank-Gulf of Maine region, which spawned on Georges Bank, southwestern Nova Scotia, and Jeffrey's Ledge (western Gulf of Maine). Lesser spawning also occurs elsewhere along the central and eastern Maine coast, near the entrance to the Bay of Fundy and in the Bay of Fundy. At the time of spawning and for the first few months of larval life, there appears to be a clear separation of the three major stocks. Thereafter, there is evidence of significant intermixing of adult fish in summer feeding and/or overwintering areas and also mixing of juveniles. In addition to the three adult herring fisheries in the region focused on the three major stocks, there are two inshore juvenile fisheries along the Maine and New Brunswick coasts, and all of these may be related.

The stock interrelationship problem is central to an understanding of the recruitment process since size of recruiting year classes are generally not known until age 2 fish are caught in the juvenile herring fisheries of the Gulf of Maine, and the earliest indication of year class strength has been the abundance of age 1 fish in the juvenile fisheries. The movements of post larval and juvenile herring from the Georges Bank stock have been the least well-documented, and this was a key reason for the focus of larval and juvenile studies on Georges Bank. Young herring (age 1) have seldom been found on Georges Bank, and they only begin to recruit to the adult fishery there at age 3 (Anthony and Waring, 1980).

Movements of adult herring (chiefly age 4+) on Georges Bank during the years 1963-1965 have been summarized by Anthony and Waring (1980). From May to October, herring were aggregated on Georges Bank for feeding and then spawning; from November to March, they occurred from Georges Bank south to 36°N. In February and March, concentrations of herring were found off Hudson Canyon and southward, and in April and May the herring moved back to Georges Bank. The extent to which adult herring from other stocks may have mixed with Georges Bank fish in the summer feeding and overwintering phases has not been determined.

Direct attempts to determine the movements and discreteness of stocks have involved larval surveys, tagging, meristic and morphometric characters, biochemical methods and parasitology (Anthony and Waring, 1980). Various biochemical methods and parasite studies have been tried, but to date none have provided a basis for definitive stock delineations in the Gulf of Maine area (Sindermann, 1979; Anthony and Waring, 1980; Anthony, 1981; Kornfield, 1984; McGladdery and Burt, 1985). Meristics, especially pectoral fin-ray counts, showed some promise at least for a time, by showing a pattern of significant difference for the 1958-1963 year classes which was consistent with the hypothesis that progeny from Georges Bank spawning were mixed with juveniles from other stocks in the Gulf of Maine, and eventually recruited back to the Georges Bank spawning stock (Anthony and Waring, 1980). The pattern did not persist, however, for the 1964-1966 year classes. The change may have been a result of colder temperatures on Georges Bank (Anthony and Waring, 1980), but in any case the later meristic evidence for racial separation was weakened.

An analysis of summer growth of age 2 herring in

Passamaquoddy Bay indicated a shift in the relationship between length increment and initial length which was coincident with the collapse of the Georges Bank fishery (Sinclair et al., 1981). The inference drawn was that Georges Bank juveniles were distributed up into the Bay of Fundy region mixed together with juveniles from other spawning populations of the Gulf of Maine area, and loss of this large source of juveniles caused the observed change in growth characteristics.

Results of extensive tagging experiments have provided perhaps the most definitive results and these have been summarized recently (Stobo, 1983). Tagging of spawning fish on the Jeffrey's Ledge and southwest Nova Scotia spawning sites has shown virtually no evidence of straying between spawning groups. However, at other times of year both adult and juvenile herring from these two major spawning stocks and other spawning groups further north in the Gulf of Maine are intermixed during their summer feeding migrations and overwintering periods (Stobo, (1983). Adults tagged off Cape Cod and in western Gulf of Maine move north and eastward in the spring and summer, and during the period April to September are distributed from the area off the central region of the coast of Maine to southwestern Nova Scotia, but with the heaviest concentrations off the central Maine coast. In late summer, the reverse movement occurs with mature fish returning to their respective spawning grounds, and then moving still further west and south during the overwintering period from November to March, with greatest concentrations of adults from western Gulf of Maine southward to Cape Cod and beyond. Juveniles tagged in the western Gulf of Maine show less extensive movements than adults, but the directions and seasonality are similar.

Herring tagged between Chedabucto Bay and southwest Nova Scotia move westward and north toward the Bay of Fundy (mainly on Nova Scotia side) in the summer, and then reverse direction with movement back to southwest Nova Scotia for spawning in October followed by eastward movement to the overwintering area off eastern Nova Scotia.

Unfortunately, collapse of the Georges Bank stock occurred before successful tagging experiments were done on that stock. The closest experiment to Georges Bank involved adult herring tagged in the spring of 1977 in the Great South Channel just west of Georges Bank; returns from these fish showed movement to the north and east, primarily into western Gulf of Maine, but a few as far east as southwest Nova Scotia during the summer. It was inferred that these fish most probably had overwintered primarily south of Cape Cod (Anthony and Waring, 1980).

The most recent interpretations of movements and interrelationships of herring stocks in the Gulf of Maine region are given by Sinclair and Iles (1985), and Sinclair et al. (1985). They concluded that historically, summer feeding adults were distributed principally in two areas, off southwest Nova Scotia, and until the collapse of the Georges Bank stock, around the perimeter of the Bank. In late summer, these herring segregate and migrate to their respective spawning grounds which include northeast Georges Bank, Nantucket Shoals, Jeffrey's Ledge, coastal Gulf of Maine, Grand Manan, Scots Bay and southwest Nova Scotia. After spawning in late summer to autumn depending upon the spawning site, they migrate and re-aggregate in two overwintering areas, the Chedabucto Bay area in the northeast, and southwest of Cape Cod. The progeny of these various spawning groups are distributed first as larvae in the vicinity of the separate spawning sites, and eventually as juveniles from the coast of Maine into the Bay of Fundy and along the coast of southwest Nova Scotia. Distributions of post-larval herring during and immediately after metamorphosis are not well documented. However, recently metamorphosed herring have been observed in the Bay of Fundy close to the larval distribution areas in summer months. In summary, they concluded there is considerable mixing between populations at all stages of the life history except for the spawning period and the first several months of the larval stage.

Although tagging studies appear to have confirmed the discreteness of spawning populations (i.e. no straying between spawning groups based on ripe herring tagged on the spawning sites), these studies have not provided direct evidence of the source of recruits to the various spawning populations. The possibility has been suggested that some progeny of one spawning ground may eventually recruit to the spawning population at another site. However, if this type of intermixing occurs, then it would appear to be at an extremely low rate in the case of recruitment to the Georges Bank stock, in view of the failure of this stock to be re-established in more than a decade.

## DEVELOPMENT OF ICNAF LARVAL HERRING PROGRAM

The ICNAF larval herring program was initiated following a 1970 recommendation by the Assessment Subcommittee (ICNAF Redbook 1970, p. 55) to conduct "studies of the dispersal of herring larvae and early o-group fish from the main centers of spawning, especially on Georges Bank and in the Bay of Fundy . . . , to help clarify the interrelation between stocks of adult and juvenile herring . . . in subareas 4 and 5". Coordinated larval surveys were begun in September 1971, and in that year five cruises were conducted from September to mid-December covering the major spawning areas of the Georges Bank-Gulf of Maine region, and involving vessels from four nations. It was noted (Redbook, 1971, p. 51) that "these surveys will give valuable information on the relative sizes of spawning groups . . . and on immediate dispersion of larvae from spawning grounds . . . but they represent only a first step toward the solution of stock interrelationships. Studies on post-larvae and juveniles . . . their distribution, abundance and movements should be intensified . . . ".

During the first two years (1971 and 1972), surveys extended from September to December, and the basic sampling at each standard station (figure 1) consisted of paired 60 cm Bongo hauls (.505 mm and .333 mm mesh), temperature profiles and usually salinity samples at selected depths (at least surface). In February 1974, the U.S. began the February series of cruises in order to provide estimates of overwinter mortality rates, and in the autumn of 1974, 20 cm Bongos with smaller mesh sizes (.253 mm and .053 mm) were added to the standard Bongo array and $O_2$ measurements were added to hydrographic sampling on a fairly regular basis. After 1974, the .053 mm mesh was replaced with .165 mm mesh to reduce clogging. A description of the sampling methods and a data report of larval herring catches for each cruise (up through 1978) is given in Lough and Bolz (1979).

At the May-June 1974 annual meeting of ICNAF, the Environmental Subcommittee considered a U.S. proposal for a comprehensive, coordinated ICNAF program of environmental research (Circ. letter 74/23 and Res. Doc. 74/70) and recommended the establishment of an "environmental working group . . . to prepare a plan for coordinated environmental research in the ICNAF area . . . with the aim of determining the factors involved in the production of good and poor year-classes in some of the main fisheries of the ICNAF area". An environmental working group was formed under the chairmanship of Dr. E. Sandeman, and following two meetings (Redbook, 1975, pp. 91-192; ICNAF Sum. Doc. 75/7) agreed that most progress could be made ". . . looking at a single fish stock or stock complex in sufficient detail to test hypotheses about causal mechanisms". The working group suggested one or more herring stocks in the Gulf of Maine region and also consideration of major groundfish stocks on Flemish Cap, and recommended an initial focus on the Georges Bank herring stock. The Environmental Subcommittee endorsed a broad range of proposals for the Georges Bank study at the 1975 annual meeting (Redbook, 1975, p. 92) including:

i) continuation of monitoring larval abundance at least for 2 more years during first 6 months of larval life during Sept.-Dec. and Feb.-Mar.

ii) spring bottom trawl surveys for juvenile herring

iii) concerted effort to understand circulation and diffusive processes

iv) a special study to follow an isolated patch of larvae on Georges Bank "to identify processes responsible for larval loss . . . finer scale variations in growth, mortality, dispersion, feeding and vertical distribution"

v) quantitative studies of primary and secondary production

Beginning in 1975, the area of sampling was restricted to the Georges Bank-Nantucket Shoals region to allow more intensive coverage on each cruise including a finer grid over spawning sites, and the suite of observations was expanded to include neuston tows, and nutrients, chlorophyll and primary production whenever possible (Redbook, 1976, p. 141). At the 1976 annual meeting, the working group reiterated the need for information on the second half of the first year of life, but considered it unwise to abandon monitoring the fall-winter period because possible factors responsible for variation in overwinter mortality (e.g. growth rate, size, robustness of larvae as they enter the winter period) might contribute to setting year class strength even though they operate in the fall and early winter. Also, there was a reluctance to divert vessels from the spring bottom trawl surveys for juvenile herring in order to sample postlarvae, because there was still hope of developing a recruitment index from catches of age 2 herring.

Although the desirability of conducting an intensive fine-scale study of a patch of larval herring had been noted in 1975, it wasn't until 1978 that a full scale "patch study" could be organized. Biologists and physical oceanographers from five countries (U.S., Canada, Federal Republic of Germany, Poland, and USSR) and eight vessels (ALBATROSS IV, ATLANTIS II, DAWSON, LADY HAMMOND, CANSO CONDOR, ANTON DOHRN, WIECZNO and BELOGORSK) took part in the coordinated study from October through mid-November. The main objective was to identify and follow a patch of recently hatched herring larvae to provide short-term (hours and days) estimates of growth, mortality and dispersal in relation to the circulation dynamics and their biological behavior, with a view toward a quantitative understanding of mechanisms controlling their dispersal and/or retention on the bank. No herring were found on Georges Bank in 1978 and the study focused instead on a dense patch of chaetognaths in an area where young herring larvae traditionally were found. Preliminary aspects of the patch study have been summarized (Wright and Lough, 1979), but the main objective of relating dispersal to circulation dynamics and vertical movements of the organisms has not been reported on until this meeting because of time required for processing the plankton samples.

General summaries and interpretations of the results from the ICNAF larval herring surveys are contained in reports of the NAFO scientific council (NAFO SCS Doc's 80/IX/30, 80/IX/32). A number of papers have been published since then and are referenced in this synopsis.

Two other important events which significantly augmented the ICNAF larval herring program were the establishment of the Polish Plankton Sorting Center in 1977 (Res. Doc. 76/VI/115), and the MARMAP program in 1976 (Sherman, 1980). By 1976, the Sorting Center in Szczecin, Poland had begun the enormous task of sorting and identifying the invertebrate zooplankton as well as total ichthyofauna from the ICNAF series which eventually amounted to 39 cruises. By January 1980, total ichthyoplankton had been sorted for nearly all cruises, but sorting of invertebrate zooplankton (especially fine mesh) was slow and still in progress. Sorting of patch study samples sufficient for analysis was completed late in 1985 and some of these results are presented at this special session.

The MARMAP program of the U.S. became fully operational in 1977 and consisted of at least six cruises per year from Cape Hatteras to western Nova Scotia, sampling ichthyoplankton, zooplankton, hydrography and nutients/chlorophyll/primary production (Sherman, 1980). By virtue of its frequent and synoptic coverage, it supplanted the ICNAF program after 1978, and has provided annual monitoring of the distribution and abundance of herring larvae and all other ichthyoplankton throughout the region since 1977. On the basis of the MARMAP coverage, there has been no evidence of a recovery of the Georges Bank herring stock (Smith and Johnson, 1986). The general results of the ICNAF and MARMAP series have been pooled together with other data in a number of papers on the production of various trophic levels on Georges Bank and the development of new hypotheses to explain recruitment variability (Cohen et al., 1982; Sissenwine et al., 1984a; Sissenwine 1984)

## RECRUITMENT PROCESS IN ATLANTIC HERRING

Studies of factors related to recruitment success in herring go back more than a century. Hjort (1914) suggested that recruitment variability may be caused by catastrophic mortality of first-feeding herring larvae as a result of lack of suitable prey (the so-called "critical period" hypothesis), or passive transport to unfavorable areas. Cushing (1975) and Cushing and Dickson (1976) proposed that survival of first feeding herring larvae depends chiefly on the "match-mismatch" of the timing of spawning in relation to production of suitable larval food, and that recruitment variability is thus largely a function of density-independent environmental factors controlling timing of plankton blooms. In a recent critique of this "match-mismatch" theory, Sinclair and Tremblay (1984) note that much of the recent research on larval fish ecology has been conducted in relation to this theory, and studies of Atlantic herring have played a key role in development of the concepts. However, more recent studies on the recruitment process for fish in general, and herring in particular, suggest that the timing of spawning is not a key factor in generating year class variations (Sinclair and Tremblay, 1984), and that predation mortality in late larval or postlarval stages is more likely to control year class variations (Sissenwine, 1984).

Sissenwine (1984) presented a general review of recent results and current hypotheses about factors controlling recruitment. He noted that both field and laboratory studies have provided evidence that starvation of larvae is not a major mortality factor, and larval surveys have shown that recruitment is not correlated with larval abundance which implies that year class size is set after the larval stage. Instead, there is now a substantial body of evidence which indicates that predation on the late larval or post-larval stages may be the major cause of recruitment variability.

In this section, the current status of knowledge about the recruitment process for Atlantic herring is briefly summarized, with principal focus on the stocks in the Gulf of Maine region and particularly Georges Bank.

### Synopsis of Herring Life History on Georges Bank

Herring typically spawn on northeast Georges Bank and on Nantucket Shoals in late September and October (figure 2). Larvae hatch in 8-9 days at about 10°C which is close to the long term average temperatures at the bottom on these spawning sites. Larvae disperse in a net southwesterly direction at about 1-5 miles per day (Boyar et al., 1973; Bumpus, 1976), and maximum dispersal occurs by December when they are usually found covering the entire Georges Bank-Nantucket Shoals area within the 100 m contour as shown in figure 3 (Lough et al. 1985).

Larvae typically grow about 5 mm per month from initial hatching at 6 mm in September to post-larvae of 50-55 mm in June

(Lough, 1976). Metamorphosis begins at an average length of about 40 mm in April or May (Sinclair and Tremblay, 1984) resulting in a juvenile stage ("brit") which forms large feeding aggregations during summer, most probably in inshore waters from Cape Cod northward into the Gulf of Maine. By the end of the first year of life, juveniles reach a length of about 12-14 cm and become partially recruited to the juvenile fisheries along the coast (Anthony and Fogarty, 1985). They reach a length of about 20 cm at the end of their second year (Anthony and Waring, 1980), and at age 2 generally dominate catches in the coastal juvenile herring fisheries.

Maturation begins at age 3 (average of 30% for the 1960-65 year classes on Georges Bank, after Boyar et al., 1973) and most fish are mature at age 4. Georges Bank herring have a relatively high growth rate (K=0.38), shorter life span (14 years) and lower L (34 cm) than most other herring stocks in the northwest Atlantic (Anthony and Waring, 1980). Also, they have relatively high fecundity.

The growth rate of Georges Bank herring as well as those from Jeffrey's Ledge and the Maine fisheries increased substantially beginning with the 1968 year class. For Georges Bank, the calculated value of K increased from .35 for the 1960-1963 year classes to .51 for the 1968-1971 year classes, including the very strong 1970 year class (Anthony and Waring, 1980). As a result of the increased growth rate, maturation occurred earlier and fecundity at length increased (Anthony and Waring, MS 1980). An average of 57% of age 3 herring were mature during 1967-1970, and 93% of age 3 fish and all of age 4 fish were mature after 1970. These changes were believed to reflect the release from density-dependent effects on growth, maturation and fecundity as a result of the drastic decline in the Georges Bank herring population (Anthony and Waring, MS 1980; Anthony and Waring, 1980). Similar differences have persisted in more recent years for western Gulf of Maine stocks (Kelly and Stevenson, 1985).

## Age At Which Year Class Strength Is Established

It is now widely recognized that year class strength is not correlated with larval abundance for fish species in general (Sissenwine, 1984). This is true for Atlantic herring, at least for larvae up to about four months old. In the North Sea, ICES countries have used larval herring surveys to back-calculate spawning stock size and young fish surveys (primarily age one) to estimate recruitment, and it is assumed year class strength is set somewhere in between these stages. Saville and Schnack (1981) argued that lack of correlation between larval abundance and year class strength may simply be due to large sampling errors in the larval data. However, Sissenwine (1984) noted that if that was the case, then larval abundance wouldn't correlate with spawning stock size.

Extensive surveys of herring larvae (≤ 4 months old) produced by the Georges Bank and southwest Nova Scotia stocks have shown correlations between early larval abundance and size of spawning stock (Lough et al., 1985; Iles et al., 1985), but no correlation with recruitment (Lough et al., 1981; Iles, pers. comm.). Hence, it follows that year class strength must be set at a later stage.

Lough et al. (1985) concluded that egg mortality excluding predation may be less than 1 % based on studies by Pankratov and Sigajev (1973) on Georges Bank and by Cooper et al. (MS 1975) on Jeffrey's Ledge. In a study in southwestern Gulf of St. Lawrence, Messieh et al. (1985) estimated that 5 % of herring eggs were non-viable and that predation mortality from winter flounder was about 30 %. Egg loss from predation is generally considered to be substantial perhaps up to 30-70 % depending upon predator populations, but it probably was significantly lower in the 1970's than in earlier years due to relatively low levels of fish biomass. If egg mortality had been extremely high and/or variable during the 1970's, then the relation between initial larval production and stock biomass on Georges Bank would not have been observed (Lough et al., 1985).

On Georges Bank, very little is known about the distribution and abundance of herring from the late larval stage until they recruit to the fishery. Boyar et al., (1973) observed significant numbers of herring larvae on Georges Bank as late as April, just prior to metamorphosis during larval surveys conducted from 1965-1970. However, age 1 herring (i.e. older than about 7 months) have not been observed on Georges Bank and age 2 herring have only been recorded there from research vessel surveys, and then only in reasonable numbers for strong year classes (Anthony and Waring, 1980). Metamorphosed juvenile herring have been observed off the Bay of Fundy (Koeller, 1979), but their abundance and movements have not been well described (Sinclair and Iles, 1985). Late larval stages in March and April have been studied over a period of years in the estuarine and inshore waters along the coast of Maine (Graham, 1982), but so far their abundance has not been consistently related to year class success.

Year class strength does appear to be set by the end of the first year of life and more certainly by age 2 when a year class makes its largest contribution to the juvenile herring fisheries. Anthony and Waring (1980) showed a general correspondence between catches at age 2 of strong and weak year classes in the Maine juvenile fisheries, and subsequent strength of the same year classes at age 3 based on cohort analysis in all three of the adult herring fisheries in the Gulf of Maine region, including Georges Bank. Furthermore, the relative size of some of these same year classes was also indicated in the catches at age 1 in the Maine juvenile fisheries, although the correspondence was not as good as for age 2. Similar relationships hold for all the juvenile herring fisheries in the Gulf of Maine (Anthony and Fogarty, 1985).

In the opinion of most scientists, herring year class success probably is largely set before the end of the first year of life, perhaps during or shortly after metamorphosis (V. Anthony, pers. comm.), but solid evidence is not yet available for the Gulf of Maine stocks. Graham (1982) obtained a significant correlation (.82) between spring (March-April) catches of late stage (pre-metamorphosed) larval herring in inshore waters of the Gulf of Maine, and catches of age 2 herring in the Maine juvenile fisheries for the 1964-1973 year classes which would imply that the year class was set just prior to metamorphosis. He also reported a significant correlation (.74) for December larval catches for the same year classes, suggesting it could even be earlier. However, for the 1974 and subsequent year classes the correspondence was not maintained. Subsequent attempts (M. Fogarty, NEFC pers. comm.) to correlate these spring larval indices with VPA estimates of year class strength for the western Gulf of Maine population have not been succesful.

Graham (1982) has postulated that the overwinter mortality rate of herring larvae might provide a clue to recruitment potential of a year class, but so far that index has not provided reliable recruitment predictions. Only a few spring (February) larval herring surveys were conducted on Georges Bank prior to the stock collapse, and although some variation in overwinter mortality was noted (notably a significantly lower "December to February" mortality rate in the '75-'76 season compared with the previous two seasons; Lough, 1976), there was no subsequent recruitment from any of these year classes to Georges Bank.

Sissenwine (1984) compared the overall mortality in the egg and larval stage (to 5 months) of Georges Bank herring to the postlarval mortality (5 months to age 2) for the period 1971-1978 and noted that the latter was higher than the former. He concluded that recruitment would therefore be more sensitive to mortality in the postlarval stage. In this instance, the start of the "postlarval" phase was based on February abundance of herring larvae which is about 2 to 3 months prior to metamorphosis. Also as noted before, the Georges Bank data represent only a few seasons with late larval estimates in February prior to cessation of spawning on eastern Georges, and thus, the results may not be representative for the species under normal conditions.

Recent ICES studies suggest that in the North Sea herring year class size may be set as early as February when fall spawned larvae are 6 or 7 months old. The February surveys have been conducted since 1976 using the IKMT (figure 4). A regression of VPA estimates of year class strength on IKMT abundance indices for the 1976 to 1983 year classes yielded an r of .76 (ICES, 1976; figure 5). With the exception of the 1979 year class which yielded a high February larval abundance index, but which turned out to be a relatively weak year class, the relationship looks promising. The herring working group is predicting good recruitment of the '85 year class partly on the basis of this regression. While it may be too early to draw firm conclusions, the results so far would suggest that in the North Sea, herring year classes may be set prior to metamorphosis in some, if not most, years.

If this is the case in the North Sea, then presumably it could also be true in the northwest Atlantic. As noted above, the data from spring surveys on Georges Bank may not be definitive. The focus of the Canadian larval surveys off southwest Nova Scotia has been on recently hatched larvae. The late spring larval studies of the western Gulf of Maine stock may not be definitive either because distribution and abundance of larvae in the inshore sampling areas probably is not representative of the entire population. This would appear to have been the case for the 1977 year class (Graham, 1982). Thus, we can't rule out the possibility that herring year class size is set prior to metamorphosis. This has important implications for the future investigation of possible factors controlling recruitment.

## Possible Mechanisms Controlling Herring Recruitment

Ultimately, it is the physical environment which controls fish abundance and presumably inter-annual variability in recruitment. If year class size were set in the early larval stage, there are many possible physical mechanisms which could directly or indirectly control survival. However, it is less apparent how physical factors might regulate predation on post-larval stages (Sissenwine, 1984). Nevertheless, there is statistical evidence that the same environmental factors may be controlling herring recruitment each year throughout the Gulf of Maine region. This is implied because there is general coherence among the strong and weak year classes (figure 6) for all three major herring stocks in the Gulf of Maine (Anthony and Waring, 1980; Anthony and Fogarty, 1985). Coherence among strong year classes might be explained by intermixing between the stocks, but not weak year classes in all the fisheries (Anthony and Waring, 1980). Despite this clue, it has proved extraordinarily difficult to establish definitive links between the environment and recruitment variability in herring.

Sissenwine (1984) noted there were two general approaches to studying recruitment mechanisms, empirical and process-oriented. The empirical approach involves fitting statistical relationships between recruitment and physical and associated biological variables, and the process-oriented approach attempts to identify causes of mortality at various life stages during the pre-recruit phase. It is useful to consider the status of knowledge on herring recruitment mechanisms within the context of these two approaches.

## Empirical Approaches

Anthony and Fogarty (1985) reviewed the literature on environmental effects on herring recruitment and noted that indices of herring year class strength in the northwest Atlantic have been statistically related to water temperature (Lett and Kohler, 1976; Sinclair et al., 1982a), wind strength and/or direction (Sinclair et al., 1982a), sea level (Sinclair et al., 1982a) and interactions with mackerel (Winters, 1976; Lett and Kohler, 1976; Skud, 1982). Also, significant correlations between water temperature and herring landings were reported by Dow (1977) and Sutcliffe et al. (1977). In none of the above cases where herring recruitment or landings were related to physical variables was there confirmation of the actual mechanism linking the biological effect with the physical variable, nor to my knowledge were any of the relationships developed into a reliable predictive equation.

In the case of interactions with mackerel, Winters (1976) inferred that recruitment in the southern Gulf of St. Lawrence herring stock was controlled by density-dependent intra-specific effects (competition and cannibalism at high levels of herring biomass), interspecific effects with mackerel (predation and competition by mackerel on larval herring) and temperature effects (with warmer temperatures favoring recruitment and high abundance of mackerel). Lett and Kohler (1976) developed a stochastic model to study the effects of temperature, predation and competition from mackerel on recruitment of herring in the Gulf of St. Lawrence, but the time series was too short to confirm any links with mackerel interactions and temperature.

Grosslein et al. (1980) reported very little direct evidence of predation on Georges Bank herring larvae by either mackerel or herring. Maurer (1976) noted the overall similarity in diet of mackerel and herring in the Gulf of Maine region, a necessary if not sufficient condition for competitive effects. However, Sissenwine et al. (1982) applied the Gause competition model for all the major fish stocks on Georges Bank and found no valid statistical evidence of population interactions. Although extremely strong year classes of herring and mackerel have not co-occurred (1960 for herring and 1967 for mackerel), both herring and mackerel had strong year classes in 1961 and again in 1966. In terms of overall trends in biomass for the entire Cape Hatteras to Labrador region, mackerel biomass reached a peak of about 1.8 million tons in 1970 following recruitment of the 1966 and 1967 year classes, and then declined steadily to less than 0.5 million tons in the late 1970's, and then showed a slight recovery by 1983 (figure 7, Anonymous, 1985). Herring biomass from Cape Hatteras to the Nova Scotia region also declined from a peak of about 900,000 tons in the late 1960's to a low level around 200-300,000 tons in the late 70's and appears to have recovered only slightly in the early 80's (figure 8, Fogarty and Clark, 1983). These population trends which are largely parallel, provide no indication that mackerel abundance inhibits herring recruitment.

Recruitment failure at very low levels of spawning stock has long been a matter of concern and conjecture. In the case of herring, the collapse of the Georges Bank stock and also herring stocks in the North Sea in prior years, has made it rather obvious that if a stock is driven down to an extremely low level, there probably is very little chance of good recruitment. Recent studies of the other stocks in the Gulf of Maine region have added further evidence which is consistent with this pattern. Graham et al. (1984) noted that catches of larval herring along the Maine coast declined abruptly in 1978 coincident with an increase in catches of adult herrring in the western Gulf of Maine fishery (Jeffery's Ledge) and its extension northward along the Maine coast. Reduced larval production persisted after 1978 and in 1981 reached its lowest level observed since 1964, and was followed by collapse of the juvenile fishery in 1983. The authors concluded that there has been a substantial decline in spawning stock in western Gulf of Maine and suggested it may be near the critical minimum level.

Anthony and Fogarty (1985) examined long term trends in recruitment to the Maine juvenile herring fisheries in relation to temperature and spawning stock in the Gulf of Maine for the period 1915-1967. They examined correlations between sardine production in a given year (index of recruitment) and production 3-5 years earlier (index of spawning stock), and obtained a significant stock recruitment relation with a lag of 4 years which in turn appeared to be influenced by temperature (figure 9). They noted, however, that the analysis did not consider possible density-dependent effects and that it was not possible to separate the effects of temperature and spawning stock. More accurate estimates of abundance at age were possible for the 1950-1978 year classes, and they fitted stock recruitment curves to two different time periods corresponding to different levels of temperature (1950-59 with higher temperatures, and 1960-1978 with lower temperatures). The results suggested two different relationships of recruitment for various spawning stock biomass levels as à function of temperature (figure 10). Still more precise measures of abundance at age based on VPA for year classes 1965-1979 were correlated with seawater temperature, salinity, sea level and Eckman transport, and only temperature provided a significant correlation. Annual temperature data was partitioned into three periods corresponding to three stages in the first year of life: (1) September-December (eggs and early larvae), (2) January-April (overwintering-late larval period), and (3) May-August (early juvenile phase). For each period, the mean, minimum and maximum monthly temperatures were computed and correlated with recruitment estimates based on VPA. Temperature data corresponded to the first year of life for the 1965-1979 year classes. Significant correlation coefficients were obtained for the mean and minimum temperatures during January-April and the minimum monthly temperature during May-August, suggesting an inverse relation between temperature and recruitment. A multiple regression of recruitment on the minimum water temperatures for the January-April and May-August periods was significant ($p<.02$) with a multiple correlation of 0.70. Thus, the authors concluded that the late larval-early juvenile period may be most critical in the establishment of year class strength. These results seem consistent with those of Graham (1982) who reported an inverse relation between winter mortality of herring larvae and minimum winter temperatures in Maine estuaries.

Anthony and Fogarty (1985) offer a plausible explanation for such a temperature effect in that lower winter temperatures and a concomitant delay in larval herring development might result in better correspondence between late larval food requirements and peak abundance levels of major copepod prey, particularly (*Calanus*) with peak abundance in March-April, and (*Pseudocalanus*) which reaches peak abundance somewhat later (Sherman et al., 1976). Observations on growth, feeding and mortality of herring larvae on Georges Bank during three winters (1974, 1975 and 1976) are not inconsistent with this suggestion (Lough et al., 1981; Cohen and Lough, 1983), but the data series is not sufficient to test the hypothesis.

Anthony and Fogarty (1985) went on to discuss the discrepancy in the statistical relationships of temperature vs recruitment for the different time periods of their study in relation to possible interactions with mackerel which had been suggested earlier by Skud (1982). Skud (1982) examined the historical mackerel and herring catch statistics dating back to the early 1800's, and he noted that herring abundance was positively correlated with temperature when herring were more abundant than mackerel, but negatively correlated when mackerel were more abundant or when the populations were shifting. The same pattern was observed in the analysis by Anthony and Fogarty (1985). They found an inverse relationship between water temperature and recruitment during the recent period (1965-1981) when mackerel were generally more abundant than herring. However, in the 1940's and 1950's when herring were more abundant than mackerel, they found a positive relationship between abundance and temperature. Despite the intriguing correspondence of the two data series, they could not offer any specific biological rationale to explain such a relationship.

Inverse correlations between herring year class strength and temperature have also been reported by Postuma and Zijilstra (1974) for the North Sea and by Bowers and Brand (1973) in the North Irish Sea. While these and the results from the northwest Atlantic are interesting, it is most likely that the effects of temperature on recruitment are confounded by biological processes and other physical variables which have not yet been clarified. Competition as well as predation and other density-dependent effects may be involved, e.g. the effects of environment and population density on growth, maturation and fecundity. Effects of temperature and stock density on these population parameters have been documented for herring and have been shown to effect egg production potential.

Anthony and Fogarty (1985) examined the relationship between growth rate of juvenile herring in the Gulf of Maine and temperature and abundance. Multiple linear regressions were fit to mean length at age 2 on cumulative temperature during the first and second growth periods (i.e. June-October during the first and second years of life) and abundance at age 2 from VPA for the year classes 1956-1976. The result showed that both temperature during the first growing season and abundance at age 2 were significantly related to mean length at age 2. Mean length at age was inversely related to year class strength, but positively related to temperature during the first growing season. Evidence for density-dependent changes in length at age 2 was obtained only when the strong year classes observed during the latter 1950's and early 1960's were included in the analysis. When only the generally weaker 1965-1979 year classes were analyzed, no significant density effect could be demonstrated, but a stronger relationship with temperature was obtained. The authors concluded that environmentally induced differences in growth rate of juvenile herring during the first year of life determine differences in size attained by the cohort at least through age 2. Growth is related to both abundance at age 2 and summer water temperature. When abundance is high, however, growth is slow regardless of temperature. Thus, density-dependent effects appear to dominate temperature-related factors in determining growth rates.

Anthony and Fogarty (1985) also summarized earlier work by Anthony (1971) who demonstrated faster growth of juvenile herring (through age 2) off western Maine than off eastern Maine. They noted that western Maine was characterized by higher summer zooplankton densities, higher mean temperatures and lower salinities than eastern Maine, and that juvenile herring growth was consistently slower in eastern Maine. It seems likely that the higher temperatures and/or greater productivity off the western Maine coast would explain the higher growth rate.

Sinclair et al. (1982b) analyzed summer growth of juvenile herring from the southwest Nova Scotia stock and found that temperature was not strongly correlated with summer growth unless a discontinuity in growth pattern (due to an apparent change in population composition of juvenile herring beginning in 1970) was taken into account. When this change was incorporated into the regression analysis, the results were not inconsistent with density-dependent growth.

Grosslein et al. (1980) reviewed the available data on diet of both predators and potential competitors of herring on Georges Bank. They noted that the most likely competitors of herring based on overlap of diet, temporal/ spatial distributions, and population size included mackerel, river herring, and sand lance. Of these, mackerel and sand lance were the only species sufficiently abundant to have been potentially significant competitors of herring. The mackerel stock was increasing in the late 1960's while herring declined rapidly, but thereafter both species declined to low levels during the 1970's. At the onset of the population "explosion" of sand lance in the middle 1970's (Sherman et al., 1981), the Georges Bank herring stock had already collapsed. Virtually all other fish species were declining along with herring during the late 1960's and first half of the 1970's, and thus competition seems unlikely to have caused the decline in herring.

Available information on predators of herring on Georges Bank was also summarized by Grosslein et al. (1980). Occurence of herring and/or clupeoids (unident.) was recorded in stomachs of many fish predators on Georges Bank, with highest frequency in cod, spiny dogfish, red hake, pollock and white hake. However, predation by the demersal stocks of fish could not have caused the herring decline because the predator stocks were also declining rapidly. Excluding mackerel and herring, the total finfish biomass declined on Georges Bank from about 3.5 million tons in 1964 to 1.2 million tons in 1975 (Clark and Brown, 1977). Squid are known to prey on herring (Vovk, 1972) and squid (*Illex*) populations increased substantially in 1976 over previous levels, but the herring were already gone.

Other important herring predators include marine mammals and large pelagics (sharks, tunas, billfishes). All of these concentrate on schooling fishes such as herring. Accurate biomass information and rates of predation for these predators are not known. However, Sissenwine et al. (1984b) speculated that marine mammals could have contributed to the collapse of the Georges Bank herring stock. They noted that the biomass of marine mammals in the range of the Georges Bank herring was sufficient to have consumed the entire population of herring that was estimated to remain after the last commercial harvest in 1977. Their estimate did not include the possible predation of the other apex predators whose fish consumption was estimated to be roughly 1/4 to 1/3 that of the marine mammals (Sissenwine, 1984; Cohen and Grosslein, in press). It is possible that predators such as these can locate the dwindling schools of declining prey population with rather high efficiency (much as fishing fleets do) and thus actually increase predation mortality rate for a given biomass of predators. This would be an example of a depensatory effect as described by Sissenwine (1984).

Disease occasionally has been responsible for drastic declines of Northwest Atlantic herring populations. A systemic fungus pathogen caused the decimation of herring stocks in the Gulf of Maine in 1932 and 1947, and in the Gulf of St. Lawrence in 1898, 1916, 1940 and 1955 (Sindermann, 1970). However, there was no evidence of this periodic epizotic during the decline and collapse of the Georges Bank stock.

## Process Oriented Studies

After the first few years, the ICNAF larval herring program evolved from its initial focus on relative size and discreteness of herring populations in the entire Gulf of Maine region to a much more ambitious program which attempted to clarify the environmental factors controlling growth, dispersal and mortality of larvae during their first 6 months of life on Georges Bank alone. The program was not developed on the basis of explicit hypotheses in relation to the "critical period" or "match-mismatch" theories, but rather on the very general hypothesis by the Environmental Working Group (ICNAF Redbook, 1975, p.91) that year class size is determined within the first year of life. Most scientists involved believed that the distribution, abundance and condition (size, robustness) of herring larvae alive after 6 months and the factors controlling these events might well provide clues to the causes of recruitment variability. However, there was a clear recognition that additional sampling of postlarval stages was also needed, especially during late spring (April/May) at the time of metamorphosis; but the necessary resources were not available to implement this phase of sampling. In any case, the collapse of the stock after only a few years of the more intensive larval studies precluded a time series sufficient for testing any hypotheses about effects of larval ecology on recruitment other than the relation between initial larval production and recruitment. Accurate estimates are not available of the strength of year classes recruiting to Georges Bank following the 1970 year class, but it is apparent they were very weak compared to the 1970 year class (Anthony and Waring, 1980). Among the 1971-1976 year classes in the other Gulf of Maine stocks, all were relatively weak except for the strong 1976 year class (Fogarty and Clark, 1983). Since 1976 was the last spawning season on Georges Bank to produce any significant number of larvae, this means only 1 out of the 6 years of larval data might have been characteristic of conditions conducive to good recruitment (assuming that the regional coherence among year classes apparent in earlier years would have continued and that only the 1976 year class would have been strong on Georges Bank under normal conditions). This doesn't provide much basis for evaluating possible significance of factors such as growth rate and overwinter mortality, since we can neither prove nor disprove hypotheses involving these factors. Nevertheless, some important features of the ecology of herring larvae $\leq$ 6 months of age on Georges Bank have been documented and these are summarized here.

## Growth, Feeding and Condition in Relation to Larval Mortality and Environmental Factors

Lough et al. (1982) fitted a Gompertz growth curve to a sample (311) of herring larvae collected on Georges Bank-Nantucket Shoals and coastal Gulf of Maine, utilizing daily growth increments on otoliths. Average growth rates based on this curve increased from 0.25 mm/day at hatching to 0.30 mm/day at 20 days, and declined to < 0.15 mm/day after 75 days of age during the winter period. The average growth rate over 150 days was 0.200 mm per day which is similar to average seasonal estimates found in most other larval herring growth studies. They noted this agrees closely with estimated average field growth rates for Georges Bank-Nantucket Shoals based on modal analysis of length frequencies from the 1971-78 ICNAF time series, which yielded an average of 0.195 mm/day for 7-30 mm size classes over 163 days (Lough et al., 1979). The form of the larval growth curve for Georges Bank appears similar to that for other herring stocks, with a slowing of growth in mid-larval stage and then increasing rapidly again at time of metamorphosis.

Cohen and Lough (1983) investigated the relation between larval herring survival and their feeding (via gut analyses of over 8000 larvae), morphological condition, and the distribution and abundance of their prey during the first 6 months of life for larvae collected on Georges Bank-Nantucket Shoals during the 1974, 1975 and 1976 spawning seasons. In these years, there were differences in production, growth and mortality as well as spawning locations, and data were available on zooplankton prey and other environmental factors. Herring larvae fed on the dominant species of copepods (*Centropages* spp., *Pseudocalanus* spp., and *Paracalanus parva*) which were the same for the entire Georges Bank-Nantucket Shoals region. In the 1975 and 1976 seasons, larvae consumed very low numbers of *Centropages* compared with 1974 and this was associated with a change in the prey species abundance and distribution at least in 1976. Adults of both species of *Centropages* virtually disappeared from the eastern half of Georges Bank during December 1975 and February 1977 compared to the same periods during the other years, and *Paracalanus parva* was very scarce in February 1974 and February 1976 and widespread but in low numbers during February 1975.

Both larval growth and survival rate increased over the autumn-winter period for the three years coincident with decreases in the overall abundance of larvae and shift in spawning areas from eastern Georges Bank to Nantucket Shoals. Age specific mortality rates estimated by Lough et al. (1981) showed that mortality was lowest in 1976 (2.2 % per day) followed by the 1975 season (2.7 % per day) with the highest in the 1974 season (3.2 % per day), whereas larval production was relatively high in 1974 ($79 \times 10^{12}$ larvae) vs $21 \times 10^{12}$ larvae in 1975 and $<1 \times 10^{12}$ larvae in 1976. Mean larval length increased during each succeeding winter over the three years, indicating that larval growth was increasing or that larger larvae were surviving in greater numbers (Lough et al., 1981). In addition, a greater percentage of feeding larvae were found in the 1976 season although they had generally lower prey numbers of smaller size and lower biomass per larva (Cohen and Lough, 1983). Also, the larvae collected in the 1976 season appeared to be more robust for their size based on a condition factor index. Thus, there appeared to be a trend of increasing growth and overwinter survival associated with the drastic decline in overall abundance of larvae. The authors could not confirm that prey fields were inadequate for normal growth in the earlier years, but they did note that estimates of prey density on Georges Bank-Nantucket Shoals were extremely low relative to estimated prey densities required for good growth by herring larvae from other studies. It should also be noted that average temperatures were quite similar in all three years for the Georges Bank-Nantucket Shoals region (average of 10-11° C in December and 6° C in February in the 0-50 m range) except that temperatures were about 1/2° C warmer in the 1974 season (Lough, 1976) which was the year of highest larval abundance and lowest growth/survival estimates.

## Temperature, Transport and Other Environmental Variables

A shift in the timing and location of the spawning was observed during the 1970's. The onset of the spawning (hatching) season occurred progressively later in the time series, ranging from mid-September to mid-October in the 1971-73 seasons, to late October-early November in the later years (Lough et al., 1981). The delayed spawning may have been related to: 1) the shift of major spawning from eastern Georges Bank to the western part of the Bank and Nantucket Shoals area where spawning is normally 1-2 weeks later, 2) the decline of larger-older fish in the population which tend to spawn earlier, and/or 3) the general warming trend in autumn bottom temperatures (Lough et al., 1981).

The later spawning has not been linked to change in larval survival, but it has been suggested tha temperatures on Georges Bank may have become high enough to impair egg development and reduce larval survival. Grimm (1983) examined bottom water temperatures at spawning sites delineated by distribution and abundance of recently hatched ($\leq$ 8 mm SL) larvae and noted that mean bottom temperatures at these sites ranged from 12° to 15° C during the first month of spawning in 1971-74, 1976 and 1977. He concluded that in view of the large volume of warm water (>13° C) on Georges Bank during October since 1971, hatching success may have been reduced since according to Blaxter (1956) hatching success tends to decline at temperatures above 12° C. Also, he noted that studies reported by Alderdice and Velsen (1971) showed Pacific herring larvae suffering mortality within 4 days after hatching at temperatures above 13° C. Grimm noted that temperatures >16° C on Georges Bank were recorded at the beginning of spawning seasons in 1971-74 and that these high temperatures could have had a deleterious effect on egg and larval survival, and/or may have contributed to the east to west shift in spawning activity from Georges Bank to Nantucket Shoals. The autumn bottom temperature on the Shoals is normally colder than on Georges Bank, and this was true particularly in 1976 and 1977 when spawning occurred principally on Nantucket Shoals.

While we cannot rule out the possibility that high temperatures may have had some deleterious effect on larval survival, there is no clear evidence to support this hypothesis. In fact, growth of larvae during the 1971-78 seasons appeared to be within normal ranges (Lough, et al. 1979). Furthermore, the correlation between larval abundance and spawning stock size (Lough, et al. 1985) would seem unlikely if unusually large and variable mortality had taken place in the egg or very early larval stages.

Circulation on Georges Bank is characterized by a clockwise mean residual flow around the crest of the bank (< 60 m) which has been postulated by many as a mechanism for retention of larval fish on Georges Bank (e.g. Boyar et al., 1973; Lough, MS 1981; Butman et al., 1982). The flow is a "leaky" gyre with northerly and northeastward components on the northern edge of Georges Bank, southeasterly and southern components on the eastern edge, and southerly and southwesterly components on the southern flank (Figure 11). Although the gyre is a persistent feature throughout the year being generally stronger in summer and weaker in winter, it is subject to periodic disruptions and variation in current speed in relation to events such as storms and warm core rings.

Lough et al. (1985) summarized the average pattern of larval dispersal from the spawning areas on Georges Bank and Nantucket Shoals and showed that larvae disperse rapidly over the shoal areas and reach the maximum extent of their distributions by late November or early December (Figure 3). During the late autumn and winter months, a mean southerly flow of surface water is evident on Georges Bank with a westerly component across the great south channel (Bumpus, 1976; Butman et al., 1982; Limeburner and Beardsley, 1982) and the general dispersal of larvae follows this pattern. Larvae from spawning areas on northeast Georges Bank typically disperse to the southwest across the bank at 2-15 km/day and intermix with larvae from Nantucket Shoals. Larger larvae are sometimes found off the northern edge of Georges Bank, in lobes extending off the northeast peak, and in slope water south of the bank. Generally, however, the bulk of the larval population is found within the 100-m isobath throughout the season. There is minimal evidence of any cross-transport of larvae between Georges Bank and Browns Bank or between Nantucket Shoals and coastal western Gulf of Maine at least during the first 6 months.

Bolz and Lough (1984) analyzed the composition of ichthyoplankton communities on Georges Bank in relation to the water mass properties (T/S) and showed that there were two faunal groups, a northern group (shelf spawners) in cooler less saline shelf water and a southern group (mesopelagic and subtropical) in warmer more saline water typical of upper slope water which bounds the southern flank of Georges Bank. From examination of the abundance of ichthyoplankton and the extent and seasonal variations in the southern faunal zone on Georges Bank based on the 1971-77 ICNAF larval cruises, they concluded that when the intrusion of slope water onto Georges Bank was absent or of limited extent, retention of larvae from spawning on the bank was apparently minimal throughout the season. In contrast, when an extensive and prolonged northward intrusion of slope water occurred, as was observed in autumn and winter of 1973 and 1974, abundance of (shelf) larvae was high, implying that conditions were favorable for their retention on the bank. They noted that strong persistent northerly winds as occurred during November, January and February of the 1976/77 season would shift the shelf/slope front southward (Ingham, 1979). Strong southerly transport of shelf water over Georges Bank in the autumn-winter of 1976-77 was indicated by the presence of water with temperatures and salinities characteristic of Gulf of Maine water (Wright, 1979) and computed Ekman transport indices (Lough et al., MS, 1979). In addition, warm core rings were present just south of Georges Bank and Nantucket Shoals in the 76-77 period which could also have generated advective loss of shelf water to the south. Bolz and Lough (1984) concluded that when the southern faunal component is missing or poorly developed, this probably indicates a significant disruption of the clockwise flow on Georges Bank, which serves as a retention mechanism for larvae spawned on the bank. They suggested that breakdown of the gyre resulting from passage of warm core rings or strong wind events could result in advective loss of shelf larvae with possible effects on recruitment.

However, with respect to larval herring, there is no direct evidence of significant advective loss south of Georges Bank since the ICNAF surveys rarely extended even to the shelf/slope front. Also as noted above, despite occassional occurrence of larger larvae found just north and east of Georges Bank, there was minimal evidence of significant northward or eastward transport off the bank (Lough et al., 1985). It might be noted that in addition to the storms of the 1976-1977 winter, the two following winters of 77-78 and 78-79 were also characterized by unusually strong northerly and northwesterly winds and also record cold temperatures (Ingham, 1982). Advective loss of herring larvae from the Georges Bank-Nantucket Shoals region may have been higher than usual in those years, but the factors which caused the extremely low production of larvae on Georges Bank (and lower production on Nantucket Shoals) in those years had already operated prior to the severe winter seasons. Thus, there is no clear evidence to suggest that advective loss of larvae was a major factor in the decline of the Georges Bank herring stock.

Dispersal away from spawning sites was discussed by Sinclair and Iles (1985) in relation to their two recent hypotheses to explain the location and timing of herring spawning. In the stock hypothesis of Iles and Sinclair (1982), both the location and mean size of spawning populations are postulated to be a function of the existence and size of geographically fixed larval retention areas. These areas exist in the tidally energetic and well-mixed water off western Nova Scotia, on Georges Bank, Nantucket Shoals and in coastal Gulf of Maine. In the hypothesis of Sinclair and Tremblay (1984) the timing of spawning at each of these sites is a function of the time necessary to complete the larval phase and yet metamorphose within the period April-October. Autumn spawning populations in well-mixed waters are adapted to conditions of slow larval development through the winter period of lower temperatures and food density, whereas spring spawning populations produce larvae in stratified waters with higher temperatures and densities of food which complete the same amount of development through metamorphosis within the same "window of time". With respect to dispersal of larvae and post-larvae, Sinclair and Iles (1985) concluded that migration to the juvenile nursery areas occurs subsequent to metamorphosis rather than during larval drift. They noted that off western Nova Scotia the northeastward drift of larvae was much less rapid than would be inferred from the surface residual currents of the area. Although not stated explicitly, the authors implied that vertical movements of larvae might be responsible for this slower dispersal, similar to the inferences drawn from estuarine studies that larval vertical migrations in relation to tidal cycles is the retention mechanism in those situations (Graham, 1972; Leggett, 1983).

In preliminary studies of vertical distribution of herring larvae off Nantucket Shoals in 1977, Potter and Lough (1980) showed that herring larvae did migrate vertically but not in a consistent pattern. In one 24-hour series, larvae were concentrated in the surface layer during both day and night hauls, but in the other series (apparently in the same population of larvae, 5-30 mm) the larvae were distributed uniformly throughout the water column both day and night. However, the mean length of larvae increased with depth in both series. Unpublished vertical distribution studies of herring larvae off Cape Cod have also shown wide distribution throughout the water column and a tendency for the larger larvae to be deeper (G. Lough, person. comm.).

Sinclair and Iles (1985) conclude that maintenance of an aggregated larval population may be essential for the successful establishment (and presumably persistence) of a spawning stock. Larvae lost from the aggregate (or as they seem to imply are dispersed so widely that density drops below some critical level) may not be able to recruit to the migrating populations subsequent to metamorphosis. Although the authors suggest no mechanism for this process, presumably the implication is that the ability to form schools after metamorphosis may be a function of the density of herring at that stage which in turn would be a function of the dispersal chiefly during the late larval stage. If this were the case, then variations in circulation could exert control over recruitment success. So far, I know of no evidence to support such a link with circulation, but neither can it be disproved.

## References

Alderdice, D. F. and F. P. J. Velsen. 1971. Some effects of salinity and temperature on early development of Pacific herring (*Clupea pallasi*). J. Fish. Res. Bd. Canada, 28:1545-1562.

Anonymous. 1985. Status of the fishing resources off the northeastern United States for 1985. NOAA Tech. Memorandum NMFS-F/NEC-42. 137 pp.

Anthony, V. C. 1971. The density dependence of growth of the Atlantic herring in Maine. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 160:196-205.

——————— 1981. The use of meristic counts in indicating herring stocks in the Gulf of Maine and adjacent waters. NAFO SCR Doc. 81/IX/127. Ser. No. N433:37 pp.

Anthony, V. C. and M. J. Fogarty. 1985. Environmental effects on recruitment, growth and vulnerability of Atlantic herring (*Clupea harengus*) in the Gulf of Maine region. Can. J. Fish. Aquat. Sci. 42:158-173.

Anthony, V. C. and G. T. Waring. 1980. The assessment and management of the Georges Bank herring fishery. Rapp. P.-V. Reun. Cons. Int. Explor. Mer 177:72-111.

Blaxter, J. H. S. 1956. Herring rearing-IV. The effect of temperature and other factors on development. Mar. Res., Scotland, 5, 19 pp.

Bolz, G. R. and R. G. Lough. 1984. Retention of ichthyoplankton in the Georges Bank region during the autumn-winter seasons, 1871-77. J. Northw. Atl. Fish. Sci. 5:33-45.

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. ICES J. Cons., 35:36-51.

Bumpus, D. F. 1976. Review of the physical oceanography of Georges Bank ICNAF Res. Bull. 12:119-134.

Butman, B., R. C. Beardsley, B. Magnell, D. Faye, J. A. Vermersch, R. J. Schlitz, R. Limeburner, W. R. Wright and M. A. Noble. 1982. Recent observations of the mean circulation on Georges Bank. J. Phys. Oceanogr. 12:569-591.

Clark, S. H. and B. E. Brown. 1977. Changes in biomass of finfishes and squids from the Gulf of Maine to Cape Hatteras, 1963-74, as determined from research vessel survey data. Fish. Bull. U.S., 75:1-21.

Cohen, E. B. and M. D. Grosslein. In press. Production on Georges Bank compared with other shelf ecosystems. In Georges Bank, ed. R. Backus. MIT press.

Cohen, E. B., M. D. Grosslein, M. P. Sissenwine, F. Steimle, and W. R. Wright. 1982. Energy budget of Georges Bank. Can. Spec. Publ. Fish. Aquat. Sci. 59:95-107.

Cohen, R. E. and R. G. Lough. 19983. Prey field of larval herring (*Clupea harengus*) on a continental shelf spawning area. Mar. Ecol. Prog. Ser. 10:211-222.

Cushing, D. H. 1975. Marine ecology and fisheries. Cambridge Univ. Press, Cambridge. 278 p.

Cushing, D. H. and R. R. Dickson. 1976. The biological response in the sea to climatic changes. Adv. Mar. Biol. 14:1-122.

Dow, R. L. 1977. Effects of climatic cycles on the relative abundance and availability of commercial marine and estuarine species. J. Cons. Perm. Int. Explor. Mer 37(3):274-280.

Fogarty, M. J. and S. H. Clark. 1983. Status of Atlantic herring resources in the Gulf of Maine region--1983. Nat. Mar. Fish. Serv., Woods Hole Laboratory. Ref. Doc. No. 83-46.

Graham, J. J. 1982. Production of larval herring, (*Clupea harengus*), along the Maine coast. J. Northw. Atl. Fish. Sci. 3:63-83.

Graham, J. J., B. J. Joule, C. L. Crosby and D. W. Townsend. 1984. Characteristics of the Atlantic herring (*Clupea harengus L.*) spawning population along the Maine coast, inferred from larval studies. J. Northw. Atl. Fish Sci., Vol 5:131-142.

Grimm, S. K. 1983. Changes in time and location of herring (*Clupea harengus L.*), spawning relative to bottom temperature in the Georges Bank and Nantucket Shoals Areas, 19971-77. NAFO Sci. Coun. Studies 6:15-34.

Grosslein, M. D., R. W. Langton and M. P. Sissenwine. 1980. Recent fluctuations in pelagic fish stocks of the northwest Atlantic, Georges Bank region, in relation to species interactions. Rapp. P.-V. Reun. Cons. int. Explor. Mer, 177:374-404.

Hjort, J. 1914. Fluctuations in the great fisheries of northern Europe viewed in the light of biological research. Rapp. P.-V. Reun. Cons. Perm. Int. Explor. Mer. 20:1-228.

ICES. 1976. Report of the herring assessment working group for the area south of 62°N. C. M. 1986/Assess:19.

Iles, T. D. and M. Sinclair. 1982. Atlantic herring: stock discreteness and abundance. Science (Wash., D. C.) 215:627-633.

Iles, T. D., M. J. Power and R. L. Stephenson. 1985. Evaluation of the use of larval survey data to tune herring stock assessments in the Bay of Fundy/Gulf of Maine. NAFO SCR Doc. 85/107.

Ingham, M. C. 1979. Marine environmental condition off the Atlantic and Gulf coasts of the United States. January 1977-March 1978. U.S. Mar. Fish. Rev. May-June 1979. p 35-47

__________ 1982. Weather conditions and trends in the Maine-Virginia coastal and offshore areas during 1970-79. NAFO Sci. Coun. Studies, 5:33-39.

Koeller, P. 1979. Distribution and movements of herring in the Bay of Fundy from juvenile surveys. Can. Atl. Fish. Sci. Adv. Comm. Res. Doc. 79/32:16 p.

Kornfield, I., B. D. Sidell, and P. S. Gagnon. 1982. Stock definition in Atlantic herring (*Clupea harengus*): Genetic evidence for discrete fall and spring spawning populations. Can. J. Fish. Aquat. Sci. 39:1610-1621.

Lett, P. F., and A. C. Kohler. 1976. Recruitment: a problem of multispecies interaction and environmental perturbations with special reference to Gulf of St. Lawrence Atlantic herring (*Clupea harengus harengus*) J. Fish. Res. Board Can. 33:1353-1371.

Limeburner, R. and R. C. Beardsley. 1982. The seasonal hydrography and circulation over Nantucket Shoals. J. Mar. Res. 40:(suppl.):371-406.

Lough, R. G. 1976. Mortality and growth of Georges Bank-Nantucket Shoals herring larvae during three winters. ICES C. M. 1976/L:37. 25 p.

__________ MS 1981. Larval fish trophodynamic studies on Georges Bank. Nat. Mar. Fish. Serv. Northeast Fish. Ctr. Woods Hole Lab Ref. Doc. No. 81-19, 42 p.

Lough, R. G. and G. R. Bolz. MS 1979. A description of the sampling methods and larval herring (*Clupea harengus*) data report for surveys conducted from 1968 to 1978 in the Georges Bank and Gulf of Maine areas. U.S. Nat. Mar. Fish. Serv. Northeast Fish. Ctr. Woods Hole Lab. Ref. Doc. No. 79-60, 230 p.

Lough, R. G., G. R. Bolz, M. D. Grosslein and D. C. Potter. 1981. 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. ICES Rapp. P.-V. 178:220-222.

Lough, R. G., M. Pennington, G. R. Bolz and A. A. Rosenberg. 1982. Age and growth of larval Atlantic herring (*Clupea harengus L.*) in the Gulf of Maine-Georges Bank region based on otolith growth increments. Fish. Bull. U.S. 80:187-199.

Lough, R. G., G. R. Bolz, M. Pennington, and M. D. Grosslein. 1985. Larval abundance and mortality of Atlantic herring (*Clupea harengus L.*) spawned in the Georges Bank and Nantucket Shoals Areas, 1971-78 seasons, in relation to spawning stock size. J. Northw. Atl. Fish. Sci. 6:21-35.

Maurer, R. 1976. A preliminary analysis of interspecific trophic relationships between the sea herring (*Clupea harengus*) and the Atlantic mackerel (*Scomber scombrus*). ICNAF Res. Doc. 76/VI/121.

McGladdery, S. E. and M. D. B. Burt. 1985. Potential of parasites for use as biological indicators of migration, feeding and spawning behavior of northwestern Atlantic herring (*Clupea harengus*) Can. J. Fish. Aquat. Sci. 42:1957-1968.

Messieh, S., R. Pottle, P. MacPherson and T. Hurlbut. 1985. Spawning and exploitation of Atlantic herring (*Clupea harengus*) at Escuminac in the southwestern Gulf of St. Lawrence, spring 1983. J. Northw. Atl. Fish. Sci. Vol 6:125-133

Postuma, K. H. and J. J. Zijilstra. 1974. Larval abundance in relation to stock size, spawning potential and recruitment in North Sea herring, p. 113-128. In J. H. S. Blaxter [ed.] The early life history of fish. Springer-Verlag, New York, Heidelberg, Berlin.

Potter, D. C. and R. G. Lough. 1980. Vertical distribution of herring larvae (*Clupea harengus L.*) on Nantucket Shoals, November 1977, collected by MOCNESS aboard Anton Dohrn 77-03. NAFO SCR Doc. 80/IX/133 (revised). Serial N207.

Saville, A. and D. Schnack. 1981. Overview -some thoughts on the current status of studies of fish eggs and larval distribution and abundance. Rapp. P.V. Reun. Cons. Int. Explor. Mer 178:153-157.

Sherman, K. 1980. MARMAP, a fisheries ecosystem study in the northwest Atlantic: fluctuation in ichthyoplankton-zooplankton components and their potential impact on the system. In Advanced concepts in ocean measurements for marine biology. F. P. Diemar, F. J. Vernberg and D. Z. Mirkes (eds.) Belle W. Baruch Inst. for Mar. Biol. and Coastal Res. Univ. S. Carolina Press, Columbia, S. C. p. 9-37

Sherman, K., C. Jones, J. Sullivan, W. Smith, P. Berrien and L. Ejsymont. 1981. Congruent shifts in sand eel abundance in western and eastern North Atlantic ecosystems. Nature 129:486-489.

Sinclair, A., M. Sinclair and T. D. Iles. 1981. An analysis of some biological characteristics of the 4X juvenile herring fishery. Proc. N. S. Inst. Sci. 31:155-171.

Sinclair, M.; T. D. Iles and W. Sutcliffe. 1982a. Herring distributions within the Scotian Shelf-Gulf of Maine area in relation to oceanographic features. ICES Sympos. on Biol. Prod. of Cont. Shelves in the Temperature Zone of the North Atlantic, March 1982, Kiel, Fed. Repub. of Germany

Sinclair, M., A. Sinclair and T. D. Iles. 1982b. Growth and maturation of southwest Nova Scotia Atlantic herring (*Clupea harengus*) Can. J. Fish. Aquat. Sci. 39:288-295.

Sinclair, M. and M. J. Tremblay. 1984. Timing of spawning of Atlantic herring (*Clupea harengus*) populations and the match-mismatch theory. Can. J. Fish. Aquat. Sci. 41:1055-1065.

Sinclair, M. and T. D. Iles. 1985. Atlantic herring (*Clupea harengus*) distributions in the Gulf of Maine-Scotian Shelf area in relation to oceanographic features. Can. J. Fish Aquat. Sci. 42:880-887.

Sinclair, M., V. C. Anthony, T. D. Iles and R. N. O'Boyle. 1985. Stock assessment problems in Atlantic herring (*Clupea harengus*) in the northwest Atlantic. Can. J. Fish. Aquat. Sci. 42:888-898.

Sinderman, C. J. 1970. Principal diseases of marine fish and shellfish. New York:Academic Press.

________________ 1979. Status of the northwest Atlantic herring stocks of concern to the United States. U.S. Dept. Comm. NOAA/NMFS. Sandy Hook Lab. Tech. Series Rept. No. 23. 449 p.

Sissenwine, M. P. 1984. Why do fish populations vary? In Exploitation of marine communities, ed. R. M. May, pp. 59-94. Dahlem Konferenzen 1984. Berlin, Springer Verlag.

Sissenwine, M. P., E. B. Cohen and M. D. Grosslein. 1984a. Structure of the Georges Bank ecosystem. Rapp. P.-v. Reun. Cons. Int. Explor. Mer., 183:243-254.

Sissenwine, M. P., W. J. Overholtz and S. H. Clark. 1984. In search of density dependence. In Proceedings of the Workshop on Marine Mammal Fisheries. Interactions of the East Bering Sea, ed. B. R. Melteff. Univ. of Alaska Sea Grant, Rept. 844-1:119-139.

Sissenwine, M. P., B. E. Brown, J. E. Palmer, R. J. Essig and W. Smith. 1982. In Mercer, M. C. [ed.] 1982. Multispecies approaches to fisheries management advice. Can. Spec. Publ. Fish. Aquat. Sci. 59:169 p.

Skud, B. E. 1982. Dominance in fishes: the relation between environment and abundance. Science (Wash. D. C.) 216:144-149.

Smith, W. G. and E. Johnson. 1986. Contrasts in distribution patterns of larval Atlantic herring in the Georges Bank area, early 1970's vs. early 1980's. NAFO SCR Doc. 86/93.

Stobo, W. T. 1983. Report of the ad hoc working group on herring tagging. NAFO SCS Doc. 83/VI/18. Sec. No. N723.

Stephenson, R. L., M. J. Power, T. D. Iles and P. M. Mace. 1985. Assessment of the 1984 4WX herring fishery. CAFSAC Res. Doc. 85/78.

Vovk, A. N. 1972. Feeding habits of the North American squid, (*Loligo pealei*) Les. Transl. Fish. Mar. Serv., Can. Transl. Ser. No. 3304.

Winters, G. H. 1976. Recruitment mechanisms of southern Gulf of St. Lawrence Atlantic herring (*Clupea harengus*) J. Fish. Res. Bd. Can. 33:1751-1763.

Wright, W. R. 1979. High salinity in the Georges Bank region in February 1977. ICES Ann. Biol. 34:34-35.

Wright, W. R. and R. G. Lough. 1979. The Georges Bank larval herring patch study of 1978. A preliminary report. ICES. C. M. 1979/L:36.

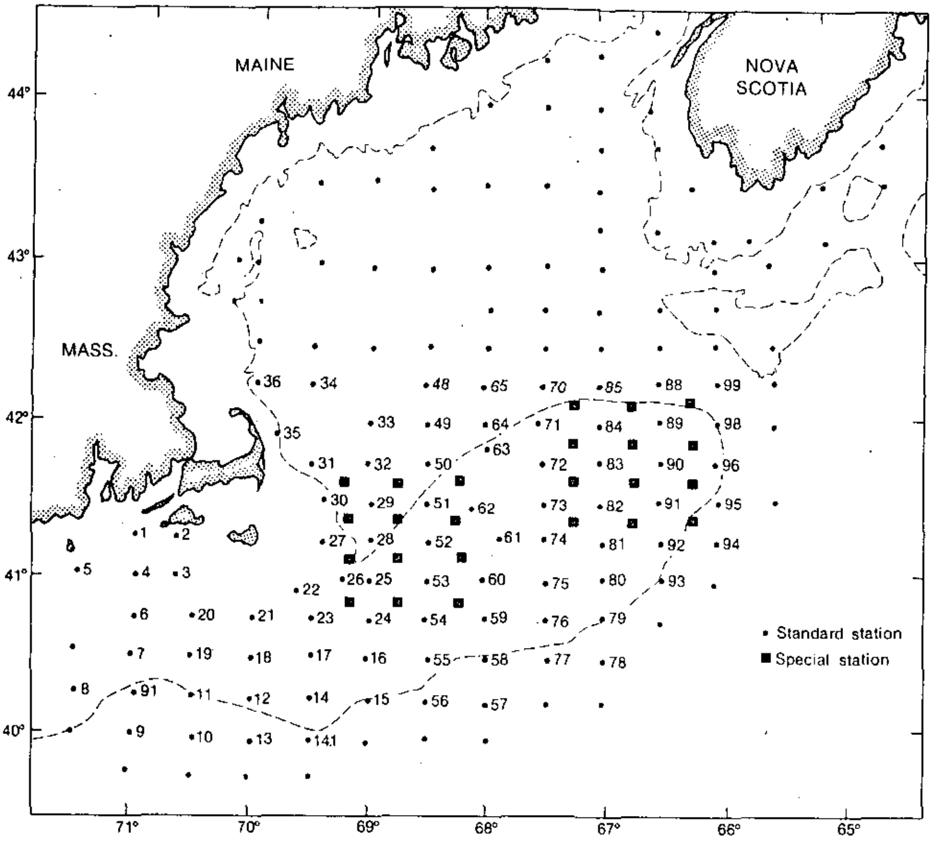

Fig. 1. Locations of standard stations for ICNAF larval herring surveys, and subset of numbered stations representative of Georges Bank (No. 48-99) and Nantucket Shoals (No. 1-36). Special stations (solid squares) were sometimes sampled in areas of high larval density. (From Lough et al., 1985.)

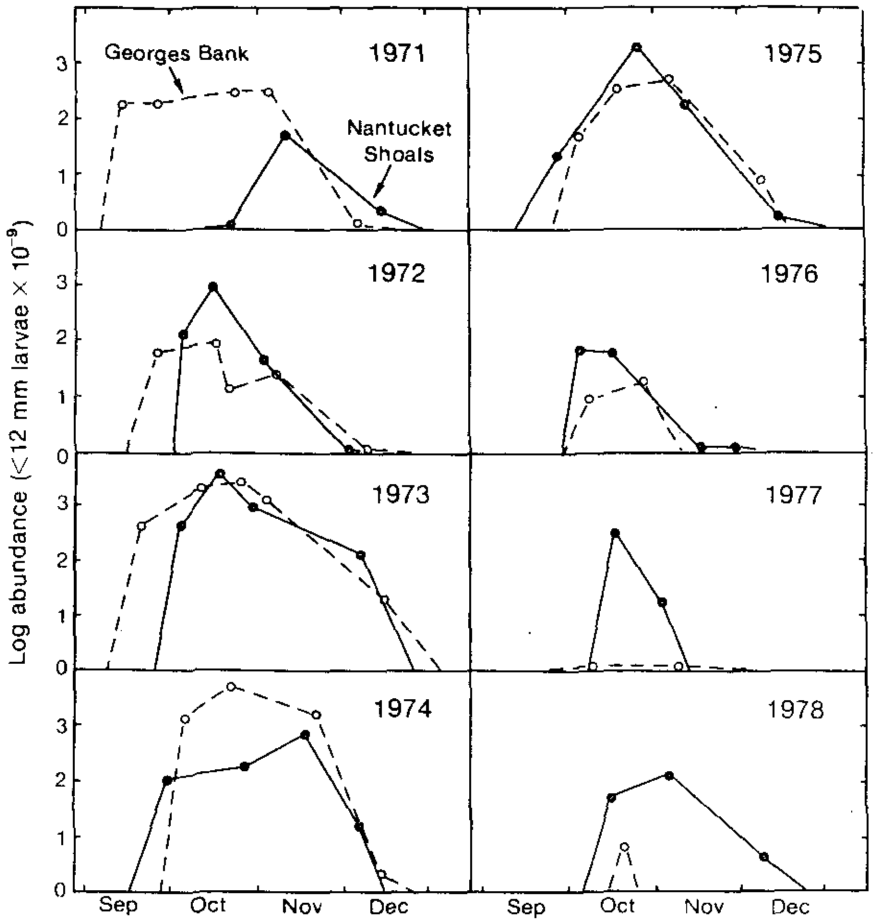

Fig. 2. Seasonal abundance of larval herring (<12 mm SL) from the Georges Bank and Nantucket Shoals spawning grounds, 1971-78. (From Lough et al., 1985.)

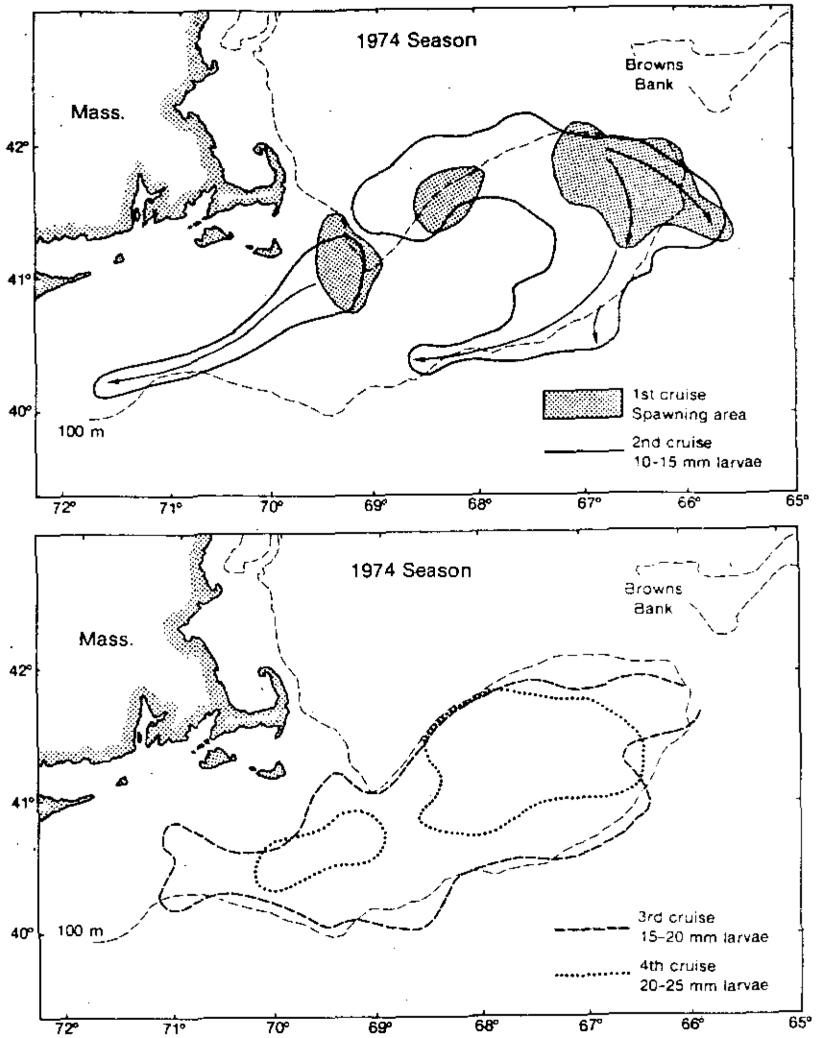

Fig. 3. Example of initial distribution (shaded) and subsequent dispersion of a cohort of larval herring from the Georges Bank and Nantucket Shoals spawning grounds over four surveys from October to December 1974. (Contours based on larval concentrations greater than $1/m^2$ for the first three cruises and greater than $0.5/m^2$ for the fourth cruise. (From Lough et al., 1985.)

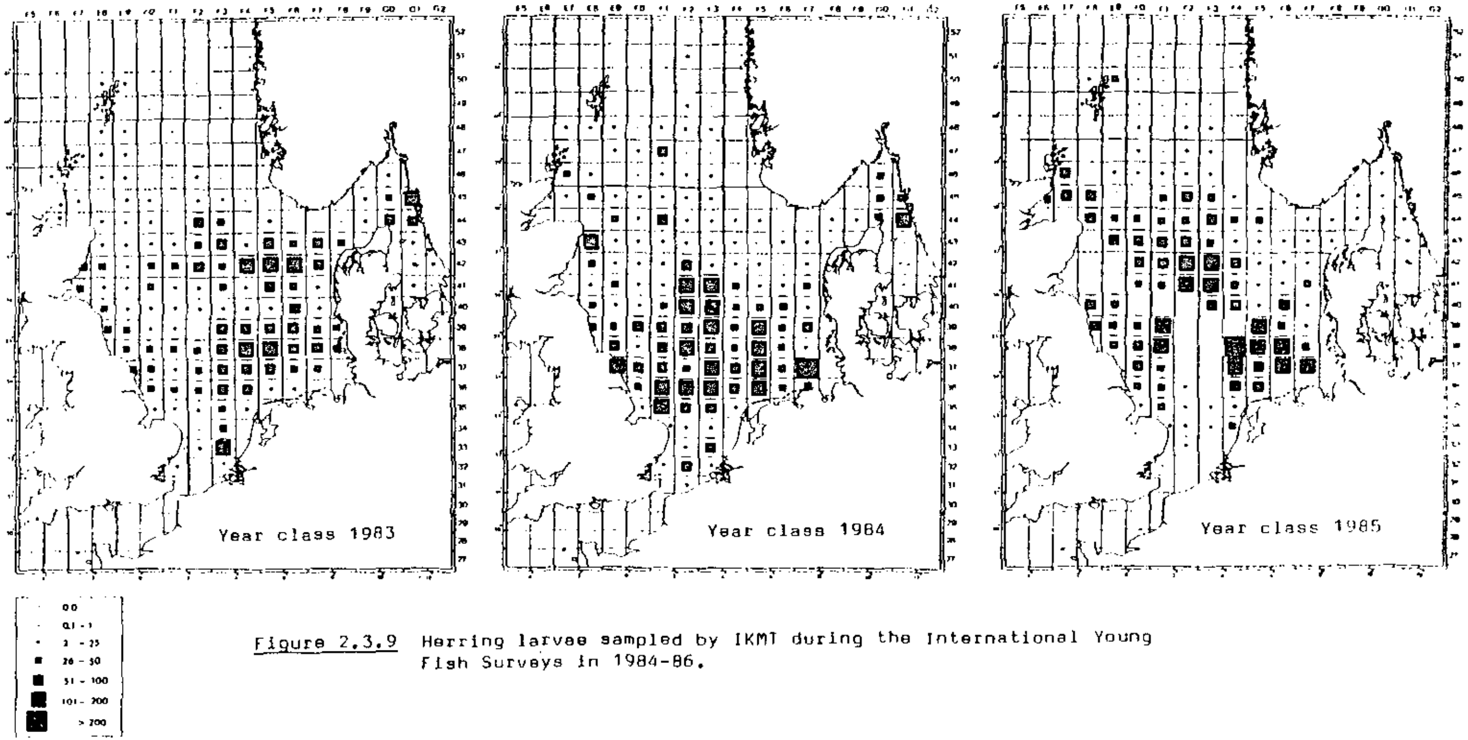

Figure 2.3.9 Herring larvae sampled by IKMT during the International Young Fish Surveys in 1984-86.

Fig. 4. Abundance indices of herring larvae caught in February IKMT surveys during the International Young Fish Surveys in 1984-1986. (figure 2.3.9,, ICES C.M. 1986/Assess:19).

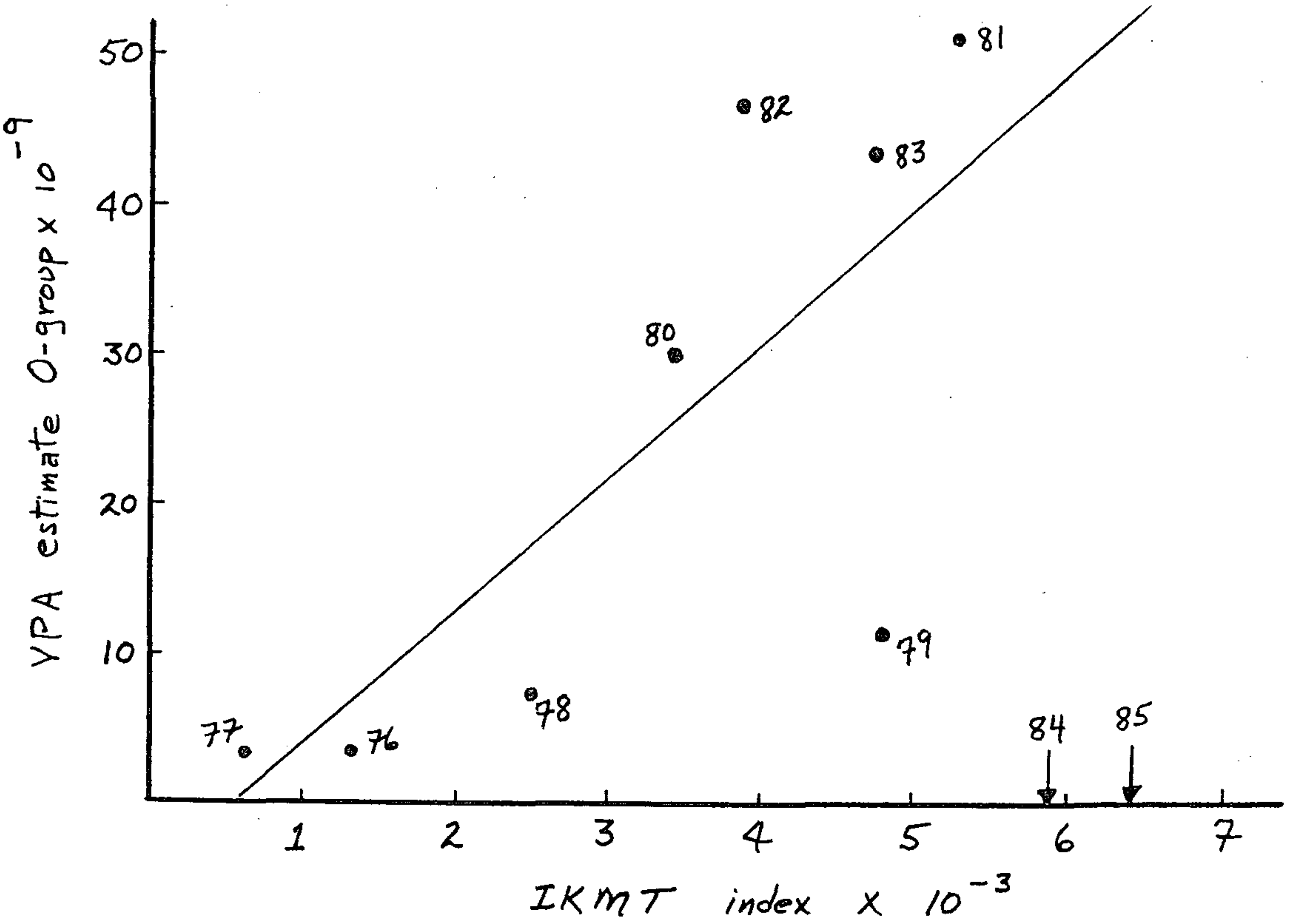

Fig. 5. Regression of VPA estimates of year class strength on IKMT indices for North Sea herring (from figure 2.3.3, ICES C.M. 1986/Assess:19).

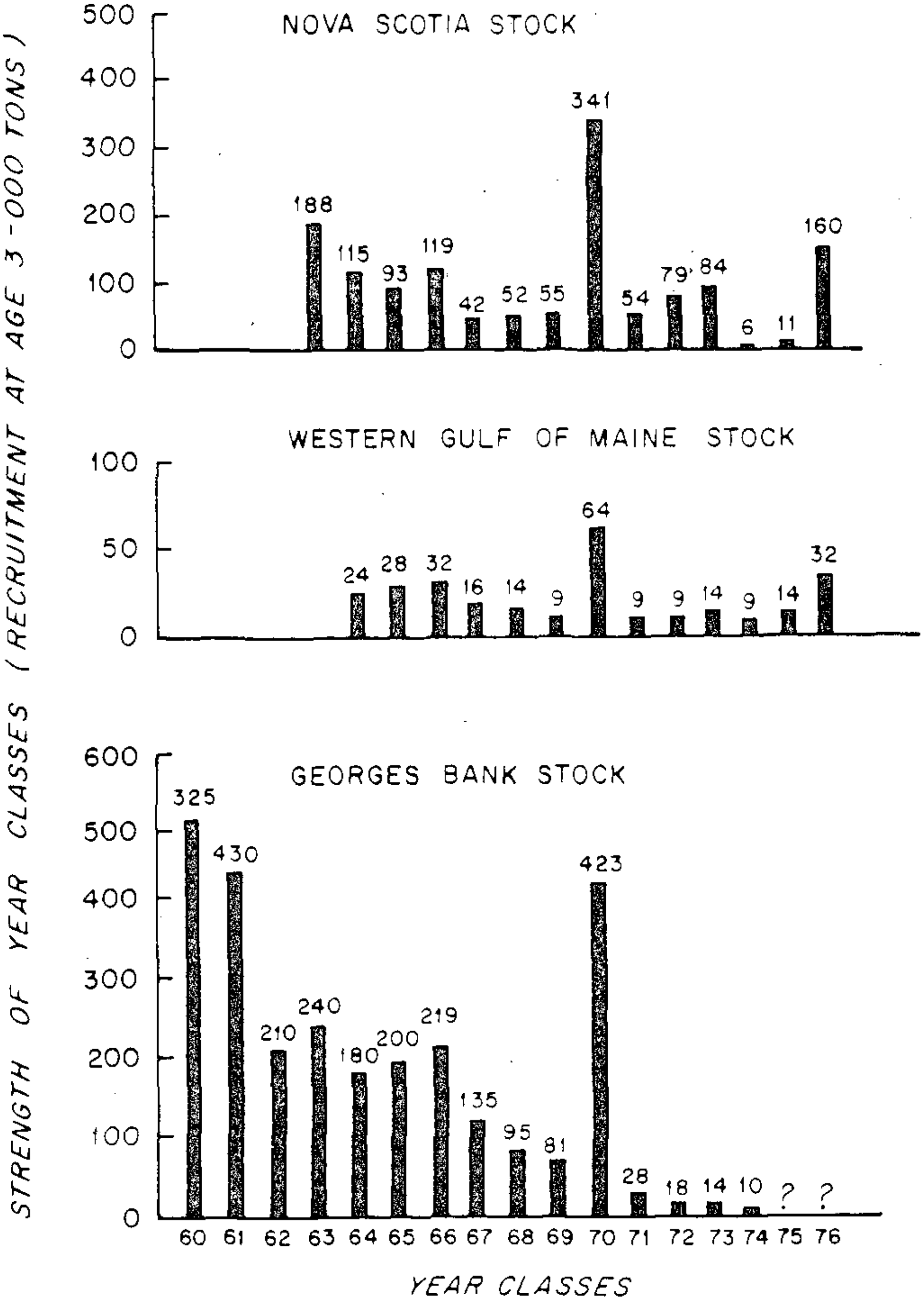

Fig. 6. Year class strength (at age 3) in Gulf of Maine adult herring stocks (from Anthony and Fogarty, 1985).

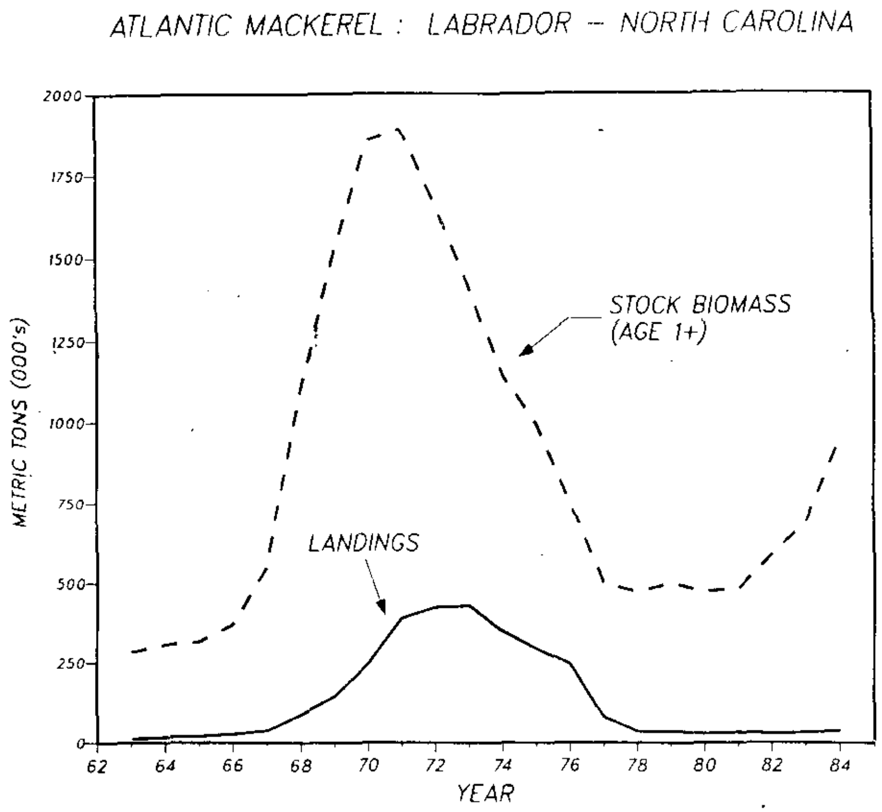

Fig. 7. Total commercial and recreational landings and estimates of stock biomass of Atlantic mackerel in the Labrador-North Carolina area.

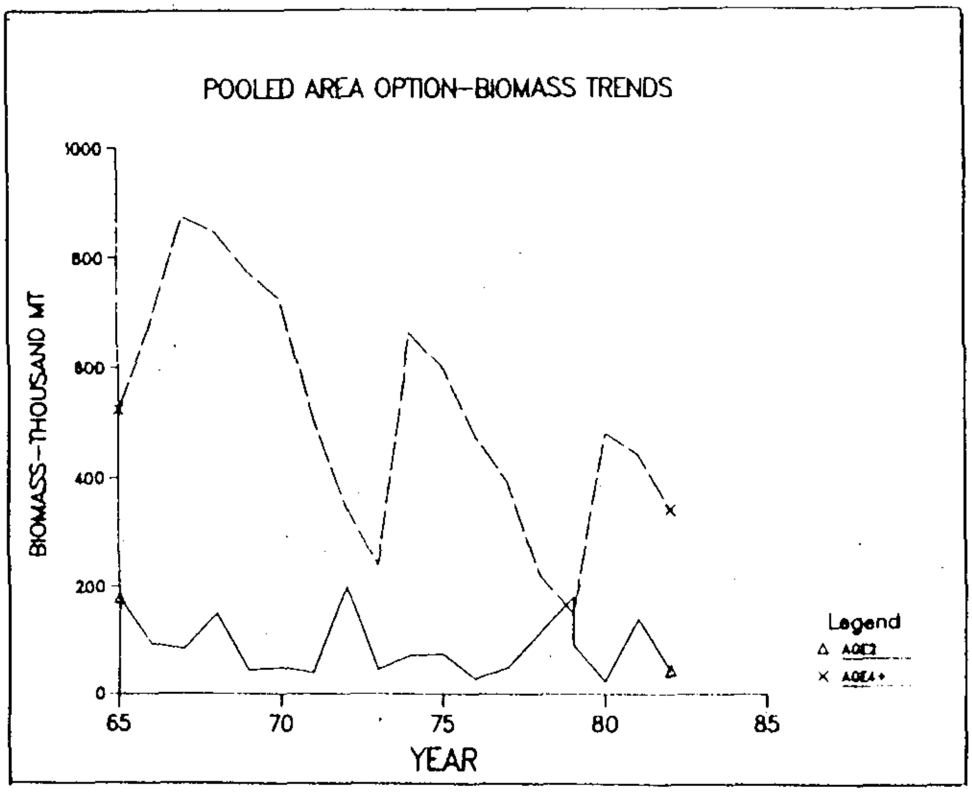

Fig. 8. Biomass trends for Atlantic herring in the Cape Hatteras-Nova Scotia region determined by virtual population analysis (from Fogarty and Clark, 1983).

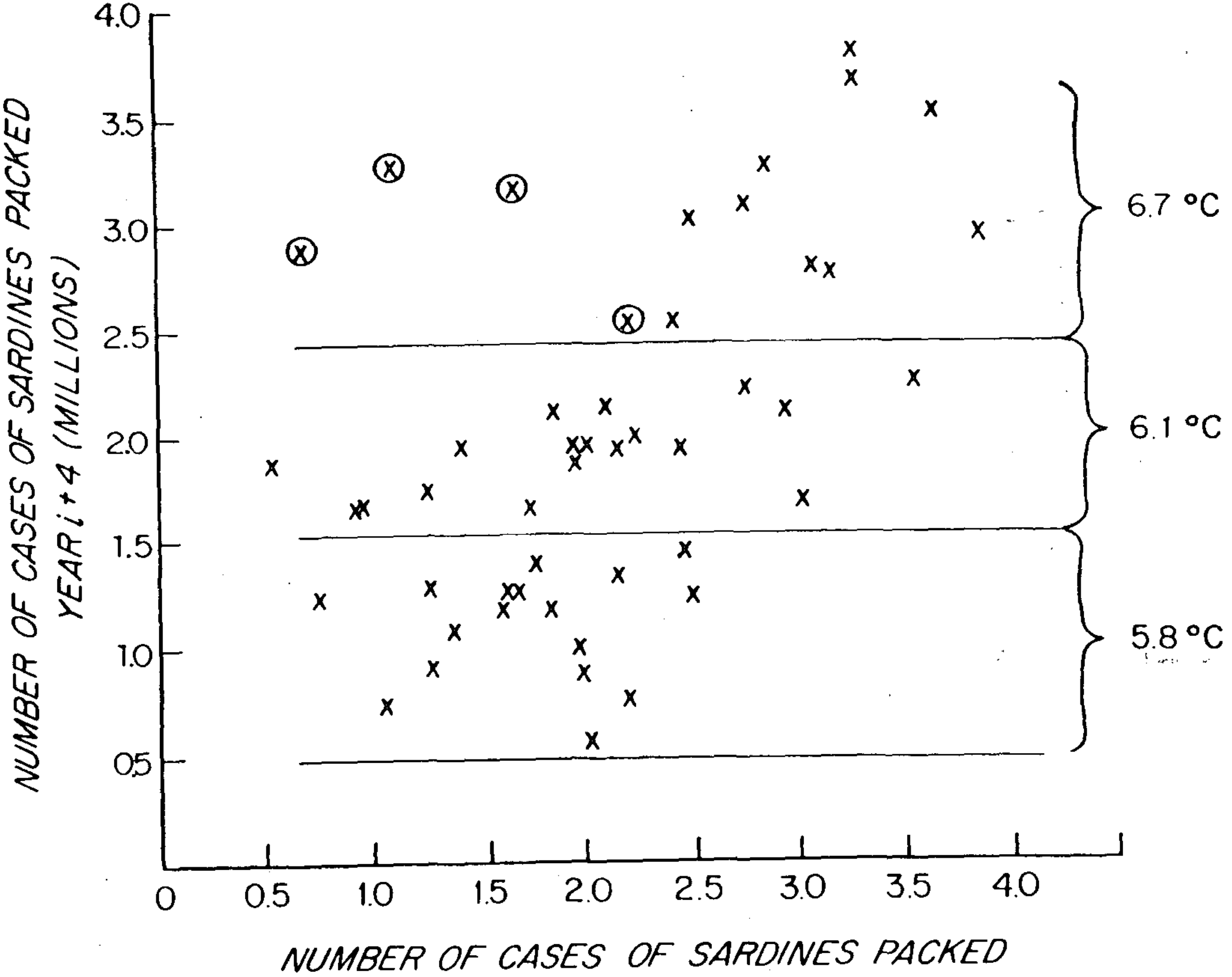

Fig. 9. Number of cases of sardines packed along the Maine coast from 1915-1967 plotted against the cases packed 4 years earlier (World War II years are circled). Water temperatures shown are averaged over September-March in year of birth (i+2). From Anthony and Fogarty, 1985.

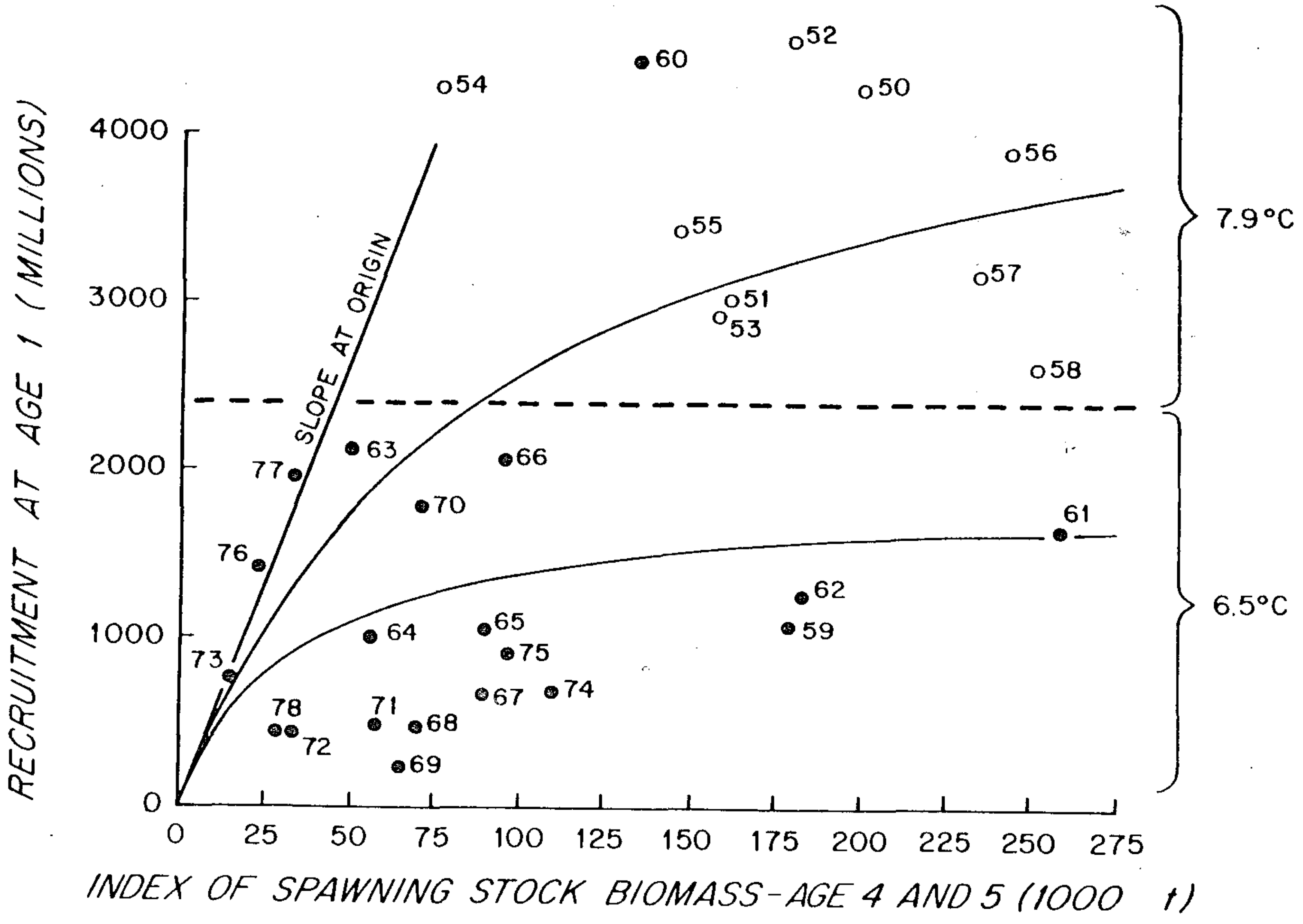

Fig. 10. Stock-recruitment curves for two time periods for Gulf of Maine herring. Temperatures are average surface water temperatures at Boothbay Harbor over September-March in the year of birth (from Anthony and Fogarty, 1985).

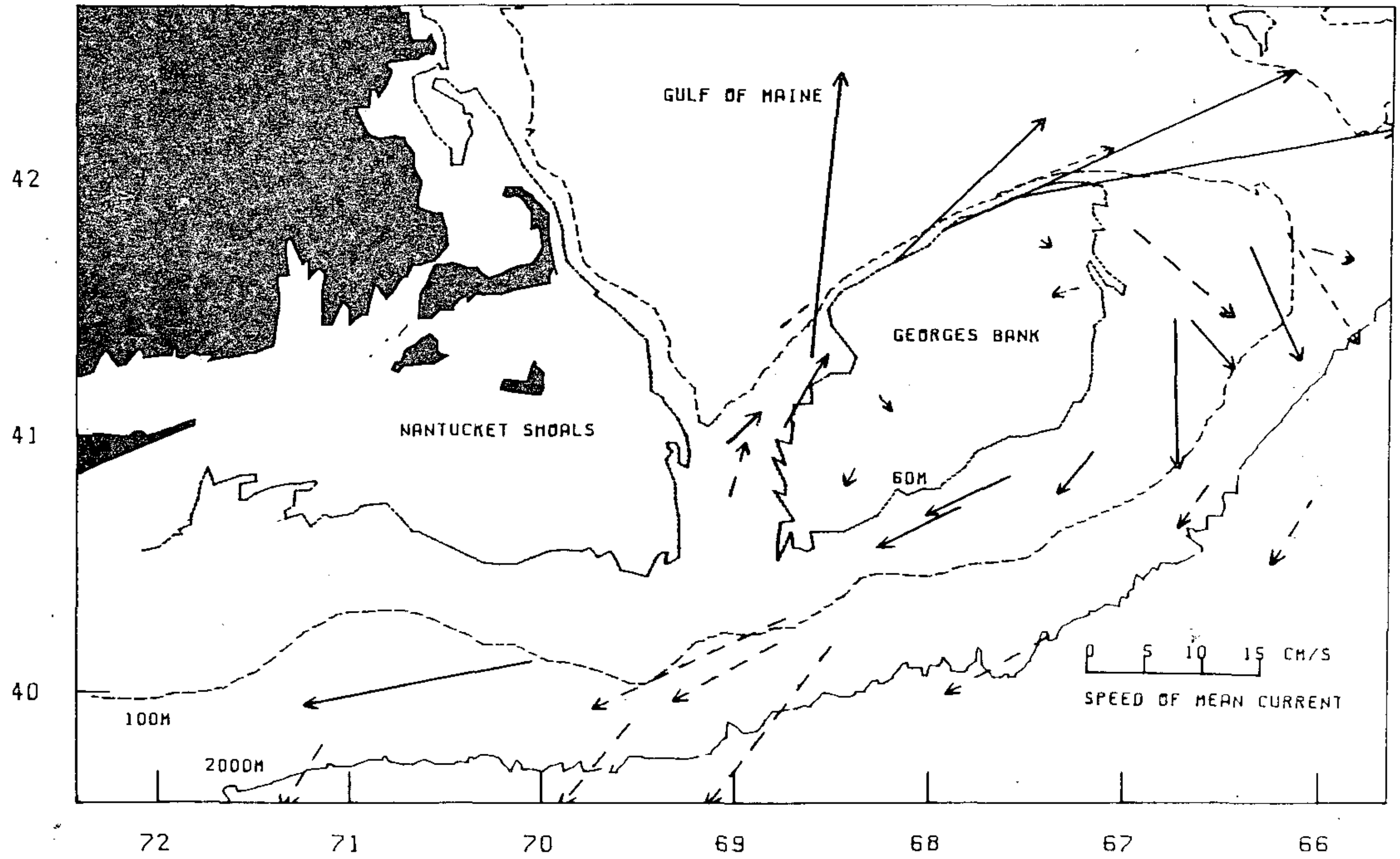

Figure 11. Mean circulation pattern on Georges Bank based on satellite-tracked drifters with drogues centered at 10 m. Measurements made during December 1978 (long dash), March 1979 (short dash) and August 1979 (solid line). (Adapted from Butman et al., 1982).