

Synopsis of Knowledge of the Recruitment Process for Atlantic Herring (*Clupea harengus*), with Special Reference to Georges Bank

M. D. Grosslein

National Marine Fisheries Service, Northeast Fisheries Center
Woods Hole, Massachusetts, 02543, USA

Abstract

An overview is presented of knowledge about the recruitment process in Atlantic herring, with major focus on the Georges Bank stock and results of the ICNAF larval herring program and other herring studies in the Gulf of Maine region. Separation of the Georges Bank spawning stock from the other major herring spawning stocks in the Gulf of Maine was confirmed by a variety of studies, including tagging and larval surveys, which showed that the spawning groups were separated at spawning time and that larval populations were discrete at least for the first few months, but considerable mixing of stocks occurred thereafter among juveniles and adults in summer-feeding and overwintering areas. A synopsis of the life history of Georges Bank herring is given and major features of the recruitment process are described with chief emphasis on possible factors controlling interannual variability in year-class success. Abundance of herring larvae (≤ 4 months old) on Georges Bank is correlated with spawning stock size but not with subsequent recruitment, indicating that major mortality factors still operate in late larval or later juvenile stages. Year-class success is definitely set by age 2 and probably even before age 1, perhaps about the time of metamorphosis. Empirical data on young herring (age 5 months to 2 years) are meager, but mortality during this period appears to be about the same magnitude as during the first 5 months, indicating that both periods are of roughly equal importance in determining recruitment variability. Both physical (density-independent) and biological (density-dependent) mechanisms are believed to control recruitment variability, but direct evidence of mortality causes in the larval and juvenile stages is largely lacking. Indirect evidence suggests that predation during the late larval and postlarval stages normally plays a major role in year-class success; starvation does not appear to be a principal mortality factor. Also, there is some circumstantial evidence that physical environmental factors may be important (e.g. advection, winter-spring temperatures during larval and early juvenile development, regional coherence in year-class success among Gulf of Maine herring stocks), but a definitive environmental link to herring recruitment has yet to be confirmed. A number of factors, ranging from direct effects of fishing to natural biotic (including epizootic disease) and abiotic mechanisms, are considered as possible causes of the collapse of the Georges Bank herring stock. So far, none appears to offer a satisfactory explanation for the virtual disappearance of the population in 1977. Regular plankton surveys on Georges Bank since 1977 have shown that there has been virtually no herring spawning in the traditional spawning areas there. Whatever the previous relationship between the Georges Bank stock and the other herring stocks in the Gulf of Maine, it is obvious that, for the past decade, there has been no recolonization of Georges Bank from these stocks.

Introduction

Rapid development of the large international fishery for adult Atlantic herring (*Clupea harengus*) on Georges Bank during the 1960's and the drastic decline in abundance of the stock in the late 1960's and early 1970's were coincident with the expansion of fishing activity on the other major groups of spawning herring in the Gulf of Maine and with a concurrent decline in the harvest of juvenile herring from coastal waters. These events, together with uncertainty and concern about the possible interrelationships 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 International Commission for the Northwest Atlantic Fisheries (ICNAF) larval herring program from 1971 to 1978 was the largest of the research 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 stocks, and to document the dispersal of larvae during their first few months in order to obtain information on possible stock interrelationships. From the beginning, it was recognized that the larval surveys represented 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 postlarvae and juveniles 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 that are needed for assessment and management. In addition to the autumn larval herring surveys, spring surveys for juveniles were also conducted in an attempt to develop recruitment indices.

The next major field program for herring was the international tagging program which was designed to determine the seasonal migrations and intermixtures 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 intermixing so that stronger inferences can be drawn about some aspects of the recruitment process for Georges Bank.

The purpose of this paper is to provide an overview of the development and results of these and other studies on Atlantic herring in the Northwest Atlantic, with emphasis on what knowledge has been acquired that is relevant to an understanding of the recruitment process. The overview 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 herring stock has received the major focus in keeping with the original intent of the special session on recruitment (NAFO, 1986), but results from other herring stocks in the North Atlantic are also included.

Stock Definitions and Movements of Herring in the Gulf of Maine Region

Three major herring stocks have been identified in the Gulf of Maine region, with spawning on Georges Bank, off southwestern Nova Scotia and on Jeffreys Ledge (western Gulf of Maine). Lesser spawning 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 during the first few months of larval life, there appears to be clear separation of the three major stocks. Thereafter, there is evidence of significant intermixing of adult herring in summer feeding and/or overwintering areas as well as mixing of juveniles. In addition to the fisheries that are focused on adult herring of the three major stocks, there are inshore fisheries for juveniles 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, because sizes of recruiting year-classes are generally not known until age 2 fish are caught in the coastal fisheries of the Gulf of Maine, and the earliest indication of year-class strength has been the abundance of age 1 fish in the fishery for juveniles. 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 studies on larval and juvenile herring of Georges Bank. Young herring (age 1) have seldom been found on Georges Bank, and recruitment to the fishery there begins with age 3 fish (Anthony and Waring, 1980).

Movements of adult herring (chiefly age 4 and older) on Georges Bank during 1963-65 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, with concentrations from Hudson Canyon southward during February and March. The herring returned to Georges Bank in April and May. The extent to which adult herring from other stocks may have mixed with Georges Bank fish during the summer-feeding and overwintering phases has not been clearly delineated.

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 attempted, but none has yet provided a basis for definitive stock delineations in the Gulf of Maine area (Sindermann, MS 1979; Anthony and Waring, 1980; Anthony, MS 1981; Kornfield *et al.*, 1982; McGladdery and Burt, 1985). Meristics, especially pectoral fin-ray counts, showed some promise at first by indicating a pattern of significant difference for the 1958-63 year-classes, which was consistent with the hypothesis that progeny from Georges Bank spawning were mixing 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 1964-66 year-classes. The change may have been the result of lower temperatures on Georges Bank, but, in any case, 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 was that the Bay of Fundy population consisted of a mixture of juveniles from the Georges Bank and other spawning populations of the Gulf of Maine region and that the loss of a large source of juveniles (collapse of the Georges Bank stock) caused the observed change in growth characteristics.

Results of extensive tagging experiments have provided perhaps the most definitive information on herring movements, and these have been summarized recently (Stobo, 1983). Tagging of spawning fish on Jeffreys Ledge and off southwestern Nova Scotia has shown virtually no evidence of straying between the spawning groups. However, at other times of the year, both adult and juvenile herring from these two major spawning stocks and other spawning groups in the Gulf of Maine are intermixed during their summer-feeding migrations and overwintering periods. Adults which were tagged off Cape Cod and in the western

Gulf of Maine moved northward and eastward in the spring and summer, being distributed during April–September from the area off central Maine to southwestern Nova Scotia, with the greatest concentrations off the central Maine coast. In late summer, the reverse occurred, with mature fish returning to their respective spawning grounds. After spawning, the adults moved westward and southward to overwintering areas, with the largest concentrations during November to March in the region from the western Gulf of Maine southward to Cape Cod and beyond. Juveniles, which were tagged in the western Gulf of Maine, showed less extensive movements than adults, but the directions and seasonality were similar.

Herring that were tagged between Chedabucto Bay and southwestern Nova Scotia moved westward and northward toward the Bay of Fundy (mainly on the Nova Scotia side) in the summer and then reversed direction, with movement back to southwestern Nova Scotia for spawning in October, followed by eastward movement to the overwintering area off eastern Nova Scotia.

Collapse of the Georges Bank herring stock occurred before successful tagging experiments could be undertaken there. The closest experiment to Georges Bank involved tagging of adult herring in the spring of 1977 in the Great South Channel just west of Georges Bank. Subsequent recaptures showed movement to the north and east, primarily into the western Gulf of Maine, but a few moved as far east as southwestern 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 were 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 southwestern Nova Scotia and, until the collapse of the Georges Bank stock, around the perimeter of that bank. In late summer, these herring segregated and migrated to their respective spawning grounds which included northeastern Georges Bank, Nantucket Shoals, Jeffreys Ledge, coastal Gulf of Maine, Grand Manan, Scots Bay and southwestern Nova Scotia. After spawning in late summer to autumn, depending upon the spawning site, the herring migrated and reaggregated in two overwintering areas: Chedabucto Bay area in the northeast, and southwest of Cape Cod. The progeny of these various spawning groups were distributed first as larvae in the vicinity of the separate spawning sites and eventually as juveniles which ranged along the coast of Maine, into the Bay of Fundy and along southwestern Nova Scotia. Distributions of postlarvae during and immediately after meta-

morphosis are not well documented. However, newly-metamorphosed herring have been observed in the Bay of Fundy close to the areas of larval distribution in the summer months. In summary, Sinclair *et al.* (1985) concluded that there was considerable intermixing of populations at all life-history stages except during 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 tagging of ripe herring on the spawning grounds), they have not provided direct evidence of the source of recruits to the various spawning populations. It is possible that some progeny of one spawning group may eventually recruit to the spawning population at another site. However, if this type of intermixing occurs, it appears 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 become reestablished during more than a decade after its collapse.

Development of the ICNAF Larval Herring Program

The ICNAF larval herring program was initiated after the Assessment Subcommittee (ICNAF, 1970, p. 55) recognized some important gaps in knowledge of the herring stocks and outlined the research requirements. There was a clear need for studies of the dispersal of herring larvae and early 0-group fish from the main centers of spawning, especially on Georges Bank and in the Bay of Fundy, in order to help clarify the interrelation between the stocks of adult and juvenile herring which were currently being exploited in Sub-areas 4 and 5. Coordinated larval surveys began in September 1971, and five cruises (involving vessels from four countries) were conducted from September to mid-December, covering the major spawning areas of the Georges Bank–Gulf of Maine region. When arrangements for the surveys were being made in early 1971, the Assessment Subcommittee noted that such surveys would give valuable information on the relative sizes of the spawning groups in the area and on the immediate dispersion of larvae from spawning grounds, but that they represented only a first step towards the solution of stock interrelationships. The Subcommittee further noted that studies on post-larvae and juvenile populations, their distribution, abundance and movements should be intensified (ICNAF, 1971, p. 51).

During the first 2 years (1971 and 1972), timing of the surveys extended from September to December, and the basic sampling at each standard station (Fig. 1) consisted of paired 60-cm bongo hauls (0.505 mm and 0.333 mm mesh), temperature profiles, and usually

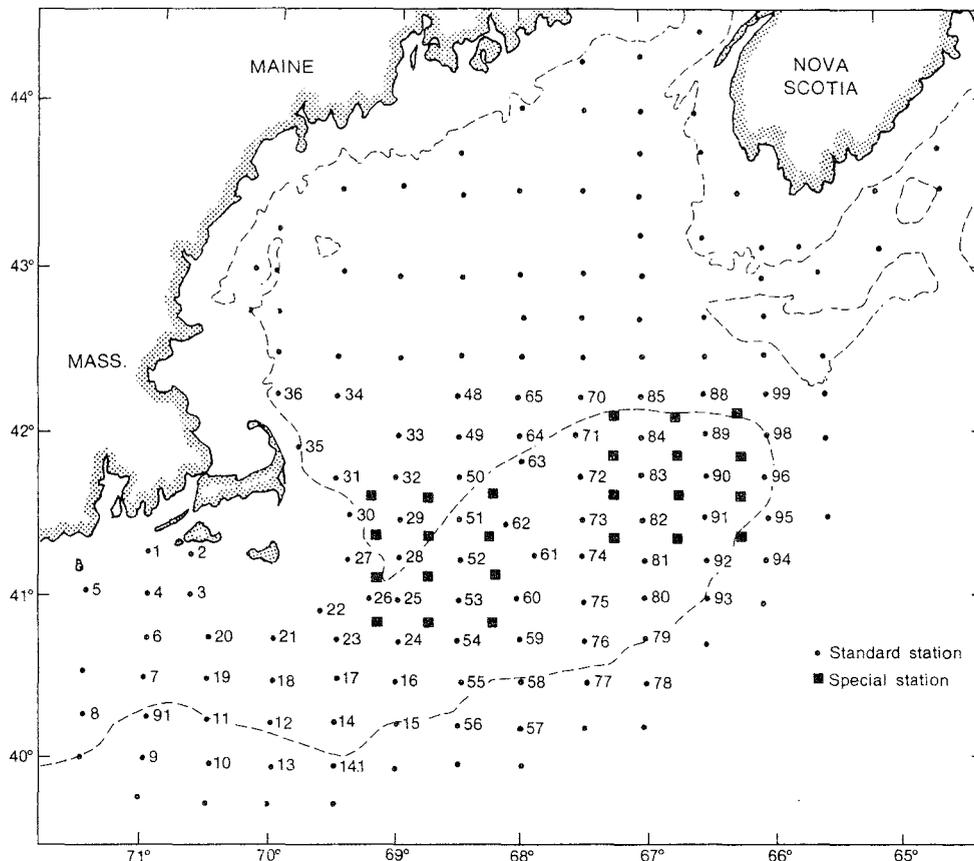


Fig. 1. Locations of standard stations for the ICNAF larval herring surveys and subset of numbered stations representative of Georges Bank (No. 48-99) and Nantucket Shoals (No. 1-36). Special stations (solid squares) were sometimes sampled in areas of high larval density. (From Lough *et al.*, 1985.)

salinity samples. In February 1974, a winter series of cruises was initiated in order to provide estimates of overwinter mortality rates. In the autumn of 1974, 20-cm bongo samplers with smaller mesh sizes (0.253 mm and 0.053 mm) were added to the standard bongo array, and oxygen (O_2) measurements were added to hydrographic sampling on a fairly regular basis. After 1974, the 0.053 mm mesh netting of the 20-cm bongo was replaced with 0.165 mm mesh netting to reduce clogging. A description of the sampling methods and a data report of larval herring catches for each cruise (to 1978) were given by Lough and Bolz (MS 1979).

At the annual meeting of ICNAF in May-June 1974, the Standing Committee on Research and Statistics (STACRES) through its Environmental Subcommittee considered a USA proposal for an expanded ICNAF program of environmental research (Schlitz and Grosslein, MS 1974) and recommended the establishment of an environmental working group to prepare a comprehensive 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 (ICNAF, 1974). Following its formation in June 1974, the working group, with E. J. Sandeman (Canada) as Convener, met

at Charlottenlund, Denmark, in September 1984 (ICNAF, MS 1975) and again at Aberdeen, Scotland, in May 1975 (ICNAF, 1975). Atlantic herring of the Georges Bank-Gulf of Maine area and Atlantic cod and redfish of Flemish Cap were selected for detailed investigations, and several research proposals were put forward to fill data gaps and to test hypotheses about causal mechanisms. Among the proposals endorsed by the Environmental Subcommittee for Georges Bank herring were: (a) continuation of monitoring larval abundance during the first 6-7 months of larval life (September-March) for at least 2 more years; (b) spring-bottom trawl surveys for juvenile herring; (c) concerted effort to understand circulation and diffusion processes; (d) a special study to follow an isolated patch of larvae on Georges Bank, with a view to identifying processes responsible for larval loss and observing finer-scale variations in growth, mortality, dispersion, feeding and vertical distribution; and (e) quantitative studies of primary and secondary production.

Beginning in 1975, the area of sampling was restricted to the Georges Bank-Nantucket Shoals area to allow more intensive coverage during each survey, including a finer grid over the spawning sites. Also, the

suite of observations was expanded to include neuston tows and sampling for nutrients, chlorophyll and primary production, whenever possible (ICNAF, 1976). At the 1976 Annual Meeting, the Environmental Subcommittee reiterated the need for information on the last 6 months of the first year of life but considered it unwise to abandon monitoring the autumn-winter abundance of larvae because possible factors responsible for variation in overwinter mortality (e.g. growth, size and robustness of larvae) may contribute to determining year-class strength (ICNAF, 1976). Also, there was 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 herring larvae had been noted in 1975, the full-scale "patch study" was not organized until 1978. Biologists and physical oceanographers from five countries and eight research vessels (*Albatross IV* and *Atlantis II* from USA; *Dawson*, *Lady Hammond* and *Canso Condor* from Canada; *Anton Dohrn* from Federal Republic of Germany; *Wieczno* from Poland; and *Belogorsk* from USSR) took part in the coordinated study during October–November. The main objective was to identify and follow a patch of recently-hatched herring larvae to provide short-term (days and hours) estimates of growth, mortality and dispersal in relation to the circulation dynamics and to observe their vertical behaviour, with a view toward a quantitative understanding of mechanisms which control their dispersal and/or retention on Georges 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 herring larvae were traditionally found. Preliminary aspects of the "patch study" have been summarized (Wright and Lough, MS 1979), but the main objective of relating dispersal to circulation dynamics and vertical movements of the organisms was not reported until recently (Lough and Trites, MS 1986) because of the time required for processing the plankton samples.

Two other important events which significantly augmented the ICNAF larval herring program were the establishment of the Plankton Sorting Center at Szczecin, Poland, in 1975 (Sherman and Ejysmont, MS 1976), and the U.S. MARMAP (Marine Ecosystem Monitoring, Assessment and Prediction) Program in 1976 (Sherman, 1980). By 1976, the Sorting Center had begun the enormous task of sorting and identifying the invertebrate zooplankton as well as the total ichthyofauna from the ICNAF herring surveys, which eventually consisted of 39 research vessel cruises. By January 1980, total ichthyoplankton had been sorted for nearly all cruises, but sorting of invertebrate zooplankton (especially the fine-mesh samples) was still progressing slowly. Sorting of the "patch study" samples, suffi-

cient for analysis, was completed in 1985, and some of these results have recently been reported (Lough and Trites, MS 1986).

The U.S. MARMAP Program became fully operational in 1977, with at least six cruises per year sampling ichthyoplankton, zooplankton, hydrography and primary production (C_{14} , nutrients, chlorophyll) from Cape Hatteras to southwestern Nova Scotia (Sherman, 1980). By virtue of its frequent and synoptic coverage, it supplanted the ICNAF program after 1978, and it has provided annual monitoring of the distribution and abundance of herring 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, MS 1986).

General summaries and interpretations of the results from the ICNAF larval herring surveys have been reported to the Scientific Council of NAFO (Grosslein, MS 1980; NAFO 1980), which replaced ICNAF in 1979. Several papers have been published since then, some of which include pooled results from both the ICNAF and MARMAP data series relevant to the production of various trophic levels on Georges Bank and the development of new hypotheses to explain recruitment variability (e.g. Cohen *et al.*, 1982; Grimm, 1983; Bolz and Lough, 1984; Sissenwine *et al.*, 1984a, 1984b; Lough *et al.*, 1985).

Recruitment Process in Atlantic Herring

Studies of factors related to the recruitment process 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 food for larvae, and that recruitment variability is thus largely a function of density-independent environmental factors controlling the timing of plankton blooms. In a recent critique of the "match-mismatch" theory, Sinclair and Tremblay (1984) noted that much of the recent research on larval fish ecology has been conducted in relation to this theory and that studies of Atlantic herring have played a key role in development of the concepts. However, more recent studies of the recruitment process for fish in general, and herring in particular, indicate that the timing of spawning is not a key factor in generating year-class variations. In a general review of recent results and current hypotheses about factors controlling recruitment, Sissenwine (1984) 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, implying that year-class size is determined after the larval stage. Instead, there is now substantial evidence which indicates that predation mortality in late larval or postlarval stages may be the major cause of year-class variations.

Synopsis of herring life history on Georges Bank

Herring typically spawn on northeastern Georges Bank and on Nantucket Shoals in late September and October (Fig. 2). The larvae hatch in 8–9 days at about 10°C, which is close to the long-term average bottom temperature on these spawning grounds. Larvae disperse in a net southwesterly direction at 1–5 nautical miles per day (Boyar *et al.*, 1973; Bumpus, 1976), and maximum dispersal occurs by December when they are usually found over the entire Georges Bank–Nantucket Shoals area within the 100 m isobath (Fig. 3) (Lough *et al.*, 1985).

The larvae typically grow about 5 mm per month from initial hatching size of 6 mm in September to postlarvae of 50–55 mm in June of the following year (Lough, MS 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 the 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 are about 12–14 cm in length and become partially recruited to the fishery for juvenile herring in coastal waters (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, they are generally dominant in the fishery for juveniles.

Maturation begins at age 3 and most fish are mature at age 4. According to Boyar *et al.* (1973), an average of 30% of age 3 fish of the 1960–65 year-classes on Georges Bank were mature. These 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.

Beginning with the 1968 year-class, the growth rate of Georges Bank herring, as well as those of Jeffreys Ledge and along the Maine coast, increased substantially. For Georges Bank herring, the calculated value of K increased from 0.35 for the 1960–63 year-classes to 0.51 for the 1968–71 year-classes, including

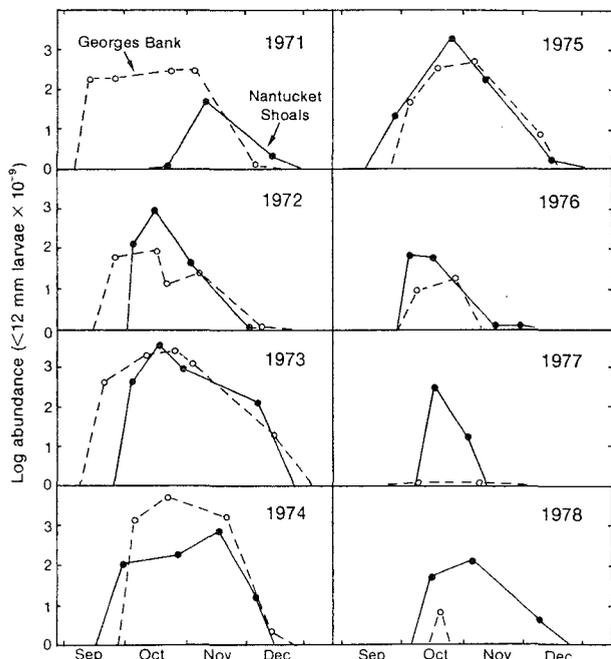


Fig. 2. Seasonal abundance of larval herring (<12 mm SL) for the Georges Bank and Nantucket Shoals spawning grounds, 1971–78. (From Lough *et al.*, 1985.)

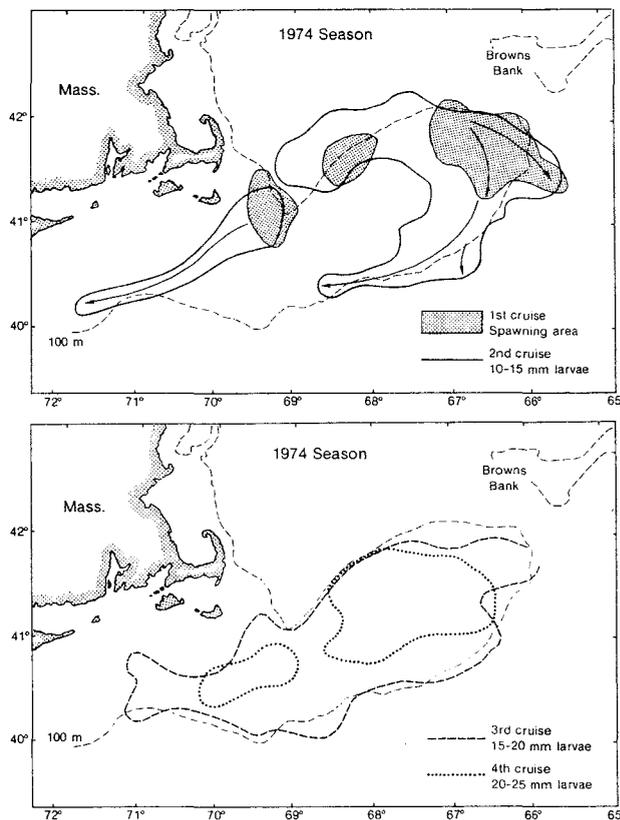


Fig. 3. Example of initial distribution (shaded) and subsequent dispersion of a cohort of larval herring from the Georges Bank and Nantucket Shoals spawning grounds over four surveys from October to December 1974. (Contours are based on larval concentrations greater than 1 larvae/m² for the first three cruises and greater than 0.5/m² for the fourth cruise.) (From Lough *et al.*, 1985.)

the very strong 1970 year-class (Anthony and Waring, 1980). As a result of the increased growth, maturation occurred earlier and fecundity-at-length increased (Anthony and Waring, MS 1980). An average of 57% of age 3 herring were mature during 1967–70, whereas 93% of age 3 and 100% 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, 1980, MS 1980). Similar differences have persisted in more recent years for the western Gulf of Maine stocks (Kelly and Stevenson, 1985).

Age when year-class strength 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 4 months old. In the North Sea, larval herring surveys are used to back-calculate spawning stock size, and young fish surveys (primarily age 1 fish) are used to estimate recruitment, it being assumed that year-class strength is set somewhere between these stages. Saville and Schnack (1981) argued that lack of correlation between larval abundance and year-class strength may be due simply to large sampling errors in the larval data. However, if that were the case, larval abundance would not correlate with spawning stock size (Sissenwine, 1984).

Extensive surveys of herring larvae (<4 months old) that were produced by the Georges Bank and southwestern Nova Scotia stocks have shown correlations between early larval abundance and size of spawning stock (Lough *et al.*, 1985; Iles *et al.*, MS 1985) but no correlation with recruitment (Lough *et al.*, 1981; T. D. Iles, Biological Station, St. Andrews, N. B., 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 Jeffreys Ledge. From studies in the southwestern Gulf of St. Lawrence, Messieh *et al.* (1985) estimated that 5% of herring eggs were non-viable and that predation mortality by fish was about 30%. Egg loss from predation is generally considered to be substantial, perhaps 30–70%, depending upon the predator populations. On Georges Bank, 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, the relation between initial larval production and stock biomass on Georges Bank would not have been observed (Lough *et al.*, 1985).

Very little is known about the distribution and abundance of Georges Bank herring from the late larval stage until they recruit to the fishery. Boyar *et al.* (1973) observed significant numbers of herring larvae as late as April (just before metamorphosis) during larval surveys on Georges Bank in 1965–70. However, age 1 herring (i.e. older than about 7 months) have not been observed on Georges Bank, and age 2 have been recorded there from research vessel surveys only when they represented strong year-classes (Anthony and Waring, 1980). Metamorphosed juvenile herring have been observed near the entrance to the Bay of Fundy (Koeller, MS 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 several years in the estuarine and inshore waters along the coast of Maine (Graham, 1982), but their abundance has not been consistently related to year-class success.

Year-class strength appears 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 coastal fishery for juvenile herring. Anthony and Waring (1980) showed a general correspondence between catches at age 2 of strong and weak year-classes in the Maine fishery for juveniles and subsequent strength of the same year-classes at age 3 from virtual population analysis (VPA) in all three fisheries for adult herring in the Gulf of Maine, including Georges Bank. Furthermore, the relative size of some of these year-classes was also indicated in the catches of age 1 herring in the Maine fisheries, although the correspondence was not as good as for age 2 fish. Similar relationships hold for all of the fisheries for juvenile herring in the Gulf of Maine (Anthony and Fogarty, 1985).

Although year-class success of herring may be largely set before the end of the first year of life, perhaps during or shortly after metamorphosis, firm evidence is not yet available for the Gulf of Maine stocks. Graham (1982) obtained a significant correlation ($r = 0.82$) between spring (March–April) catches of late stage (premetamorphosed) larvae in inshore waters of the Gulf of Maine and catches of age 2 herring (1964–73 year-classes) in the Maine fishery for juveniles, which implies that year-classes were set just prior to metamorphosis. He also reported a significant correlation ($r = 0.74$) between December catches of larvae of the same year-classes and catches of age 2 herring, implying an even earlier determination of year-class strength. However, the correspondence was not maintained for the 1974 and subsequent year-classes. Recent attempts by M. J. Fogarty (Northeast Fishery Center, Woods Hole, Mass., pers. comm.) to correlate these spring indices of larval abundance with estimates

of year-class strength from VPA for the western Gulf of Maine population have not been successful.

Graham (1982) 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 collapse of the stock, and, although some variation in overwinter mortality was noted (i.e. a significantly lower mortality rate in December–February of the 1975/76 season compared with the previous two seasons (Lough, MS 1976)), there was no subsequent recruitment to Georges Bank from any of these year-classes.

Sissenwine (1984) compared the overall mortality in the egg and larval stages (to 5 months) of Georges Bank herring to the postlarval mortality (5 months to 2 years) for the 1971–78 period 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 abundance of herring larvae in February, which is 2–3 months prior to metamorphosis. Also, as noted before, the Georges Bank data represent only a few seasons with estimates of larval abundance in February prior to the cessation of spawning on the northeastern part of Georges Bank. Thus, the results may not be representative for the species under normal stock conditions.

Recent studies in the North Sea indicate that herring year-class size may be set as early as February when autumn-spawned herring are 6–7 months old. February surveys there have been conducted since 1976 with the Isaacs-Kidd midwater trawl (ICES, MS 1986), and the abundance indices for the 1976–83 year-classes were significantly correlated ($r = 0.76$) with estimates of year-class strength from VPA (Fig. 4). With the exception of the 1979 year-class, which yielded a high larval abundance index in February but which turned out to be a relatively weak year-class, the relationship looks promising. In fact, the ICES herring working group, partly on the basis of this regression, predicted good recruitment of the 1985 year-class. While it may be too early to draw firm conclusions, the results so far indicate that herring year-classes in the North Sea may be set prior to metamorphosis in some, if not most, years. If this is the case for North Sea herring, presumably it could also be true for herring stocks in the Northwest Atlantic. As noted above, the data from winter surveys on Georges Bank may not be definitive. The focus of the Canadian larval herring surveys off southwestern Nova Scotia has been on newly-hatched larvae. The late spring larval studies in the western Gulf of Maine may not be definitive either,

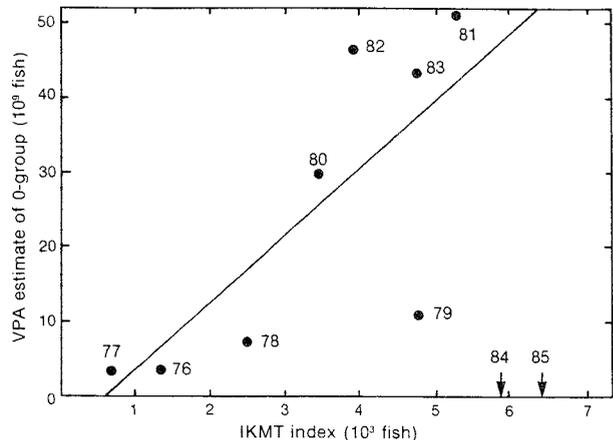


Fig. 4. Regression of VPA estimates of year-class strength on IKMT indices for North Sea herring, 1976–85. (From ICES, MS 1986.)

because distribution and abundance of larvae in the inshore sampling areas are probably not representative of the entire population. This seems to have been the case for the 1977 year-class (Graham, 1982). Thus, the possibility that herring year-class size is set prior to metamorphosis cannot be ruled out. This has important implications for future investigation of possible factors which control recruitment.

Possible mechanisms controlling herring recruitment

Ultimately, it is the physical environment which controls fish abundance and presumably interannual variability in recruitment. If year-class size is set in the early larval stage, there are many possible physical factors which could directly or indirectly affect survival. However, it is less apparent how physical factors might regulate predation on postlarval stages (Sissenwine, 1984). Nevertheless, there is statistical evidence that the same environmental factors control herring recruitment each year throughout the Gulf of Maine region. This is implied from the general coherence among the strong and weak year-classes (Fig. 5) for the three major herring stocks in the Gulf of Maine (Anthony and Waring, 1980; Anthony and Fogarty, 1985). Intermixing of the stocks might explain the coherence among strong year-classes but not the weak year-classes in all fisheries (Anthony and Waring, 1980). Despite this clue, it has been extraordinarily difficult to establish definitive links between the environment and recruitment variability in herring.

Sissenwine (1984) noted that 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, whereas the process-oriented approach attempts to identify causes of mortality at various life stages during the prerecruit phase. It is

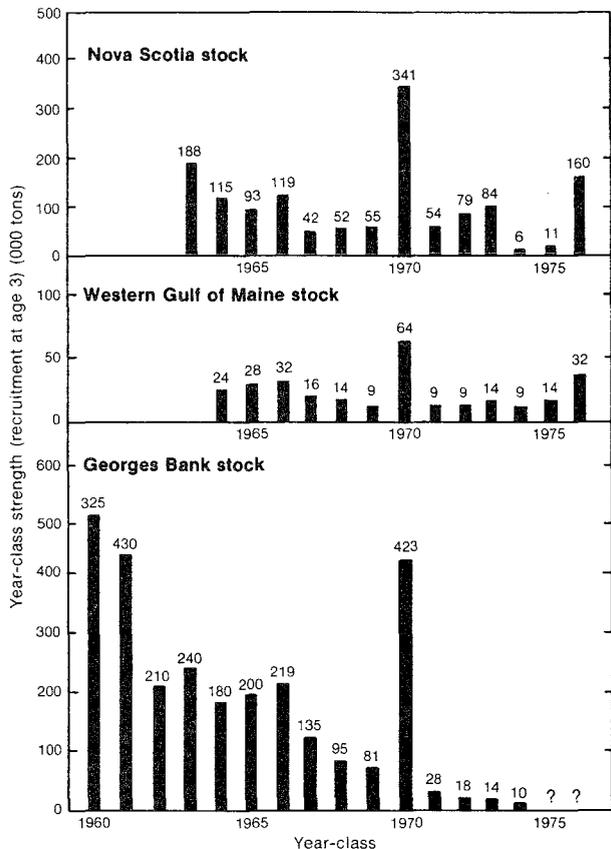


Fig. 5. Estimated year-class strength (age 3) of herring in three Gulf of Maine stocks. (From Anthony and Fogarty, 1985.)

useful to consider the status of knowledge on herring recruitment mechanisms within the context of these two approaches.

Empirical approach to studying herring recruitment

Anthony and Fogarty (1985) reviewed the literature concerning effects of the environment 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) and interactions with Atlantic mackerel (Lett and Kohler, 1976; Winters, 1976; Skud, 1982). Also, significant correlations between water temperature and herring catches were reported by Dow (1977) and Sutcliffe *et al.* (1977). In none of the cases where herring recruitment or catches (landings) were related to physical variables was there confirmation of the actual mechanism that linked the biological effect to the physical variable, nor was any of the relationships developed into a reliable predictive equation.

In the case of interactions with Atlantic mackerel, Winters (1976) inferred that recruitment in the southern Gulf of St. Lawrence herring stock was controlled by density-dependent intraspecific effects (competition and cannibalism at high levels of herring abundance), interspecific effects (predation and competition by

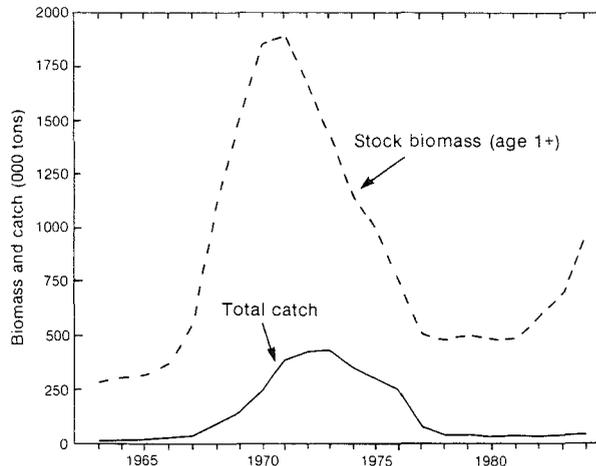


Fig. 6. Total commercial and recreational catches and estimated biomass (age 1+) of Atlantic mackerel in the region from Labrador to North Carolina, 1963-84.

mackerel on herring larvae), and temperature effects (warmer water favoring recruitment and high abundance of mackerel). Lett and Kohler (1976) developed a stochastic model to study the effects of temperature as well as mackerel predation and competition on recruitment of herring in the Gulf of St. Lawrence, but the time series was too short to confirm any link with mackerel and temperature.

Grosslein *et al.* (1980) reported that there was very little direct evidence of predation on Georges Bank herring larvae by either mackerel or herring. Maurer (MS 1976) noted the overall similarity in the diets 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 of the major fish stocks on Georges Bank and found no statistical evidence of significant population interactions. Although extremely strong year-classes of herring and mackerel have not co-occurred (1960 year-class for herring and 1967 for mackerel), both herring and mackerel had strong year-classes in 1961 and 1966. In terms of overall trends in biomass for the Northwest Atlantic (Cape Hatteras to Labrador), mackerel biomass reached a peak of about 1.8 million tons in 1970, following recruitment of the 1966 and 1967 year-classes, declined steadily to less than 0.5 million tons in the late 1970's, and then showed a slight recovery by 1983 (Fig. 6) (Anon., 1985). The biomass of herring in the region from Cape Hatteras to Nova Scotia also declined from a peak of about 900,000 tons in the late 1960's to a low level of 200,000-300,000 tons in the late 1970's and appeared to have recovered only slightly in the early 1980's (Fig. 7). 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 conjec-

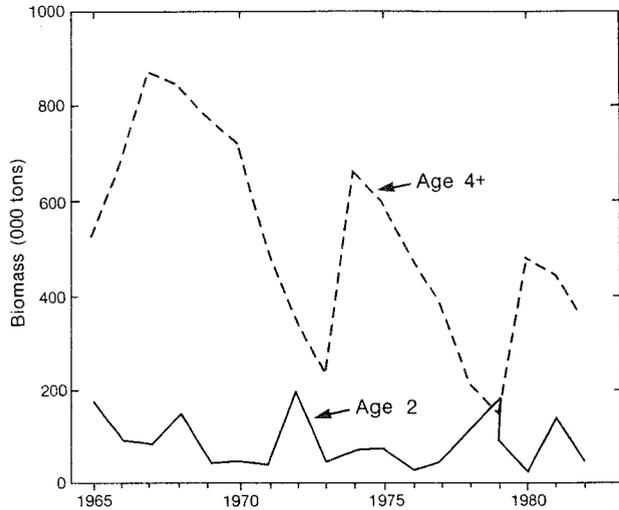


Fig. 7. Estimated biomass (from VPA) of juvenile (age 2) and adult (age 4+) herring in the region from Nova Scotia to Cape Hatteras, 1965-82. (From Fogarty and Clark, MS 1983.)

ture. In the case of herring, the collapse of the Georges Bank stock, and also the herring stocks of the North Sea in earlier years, has made it rather obvious that, if a stock is over-exploited and declines 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 herring larvae along the Maine coast declined abruptly in 1978, coincident with an increase in catches of adult herring in the western Gulf of Maine fishery (Jeffreys Ledge) and its extension northward along the Maine coast. Reduced larval production persisted after 1978 and declined in 1981 to the lowest level observed since 1964. This was followed by collapse of the fishery for juvenile herring in 1983. The authors concluded that there has been a substantial decline in the western Gulf of Maine spawning stock which may be near the critical minimum level.

Anthony and Fogarty (1985) examined long-term trends in recruitment to the Maine fishery for juvenile herring in relation to temperature and spawning stock in the Gulf of Maine for the 1915-67 period. They examined correlations between "sardine" (young herring) production in a given year (index of recruitment) and production 3-5 years earlier (index of spawning stock) and obtained a significant stock-recruitment relationship with a lag of 4 years, which in turn appeared to be influenced by average sea-surface temperature in September-March (Fig. 8). 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 by age-group were possible for the 1950-78 year-classes, and stock-recruitment curves were fitted for the two different time periods corresponding to different levels of tempera-

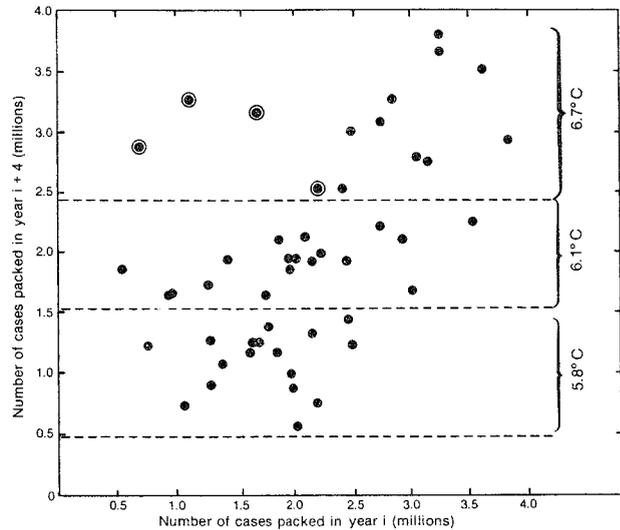


Fig. 8. Number of cases of "sardine-sized" juvenile herring packed along the Maine coast during 1915-67 plotted against number of cases packed 4 years earlier (points for World War II years are circled). Water temperatures are averages for the September-March period of egg and larval development. (From Anthony and Fogarty, 1985.)

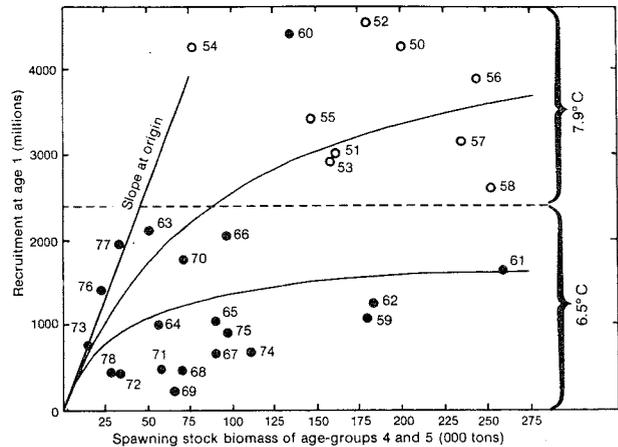


Fig. 9. Stock-recruitment curves for Gulf of Maine herring during two periods (1950-59 and 1960-78). Temperatures are averages (surface) at Boothbay Harbor, Maine, for the September-March period of egg and larval development. (From Anthony and Fogarty, 1985.)

ture (1950-59 with higher temperatures, and 1960-78 with lower temperatures) (Anthony and Fogarty (1985). The results indicated two different relationships of recruitment for various spawning biomass levels as a function of temperature (Fig. 9). However, they noted that increased availability rather than high abundance may have been the cause of higher catches during the earlier period, and thus the actual effects of temperature could not be determined.

In contrast to their results of the long-term analyses of herring abundance (or yield) and water temperature, Anthony and Fogarty (1985) found an

inverse relation based on a detailed examination of the relationship between strength of the 1965–79 year-classes and temperature, using more precise measures of abundance by age-group (based on VPA) for these year-classes. These indices were analyzed relative to water temperature and salinity, sea level and Eckman transport, but only temperature provided a significant correlation. Temperature data for each year were partitioned into three periods corresponding to three stages during the first year of life: (a) September–December for eggs and larvae, (b) January–April for overwintering and late larvae, and (c) May–August for the early juvenile phase. For each period, mean, minimal and maximal monthly temperatures were computed and correlated with recruitment estimates from the VPA. Correlations were significant for the mean and minimal temperatures during January–April and the minimal monthly temperatures during May–August, indicating an inverse relation between recruitment and temperature. A multiple regression of recruitment on minimal water temperatures for the January–April and May–August periods was significant ($P < 0.02$) with a correlation coefficient of 0.70. Thus, the authors concluded that the late larval-early juvenile period may be the most critical in the establishment of year-class strength. These results seem to be consistent with those of Graham (1982) who reported an inverse relationship between winter mortality of herring larvae and minimal winter temperature in Maine estuaries.

Anthony and Fogarty (1985) offered a plausible explanation for an inverse temperature effect, in that lower winter temperature and concomitant delay in larval herring development might result in better correspondence between late larval food requirements and peak abundance levels of copepod prey, particularly *Calanus* sp. with peak abundance in March–April and *Pseudocalanus* sp. with somewhat later peak abundance (Sherman *et al.*, MS 1976). Observations on growth, feeding and mortality of herring larvae on Georges Bank during three winters (1974–76) are not inconsistent with that view (Lough *et al.*, 1981; Cohen and Lough, 1983), but the data series is not sufficient to test the hypothesis. Inverse correlations between herring year-class strength and temperature have also been reported by Postuma and Zijlstra (1974) for the North Sea and by Bowers and Brand (1973) for the northern Irish Sea.

It seems likely that the effects of temperature on recruitment may be confounded by biological processes and other physical variables. Competition as well as predation and other density-dependent effects may be involved (e.g. population density on growth, maturation and fecundity). Effects of temperature and stock density on these population parameters (including egg production potential) have been documented for herring.

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 of mean length at age 2 on cumulative temperature during the first and second growing seasons (June–October) and abundance at age 2 (from VPA) for the 1956–76 year-classes 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 of the late 1950's and early 1960's were included in the analysis. No significant density-dependent effect could be demonstrated when only the generally weaker 1965–79 year-classes were analyzed, but a stronger relationship with temperature was noted. The authors concluded that environmentally-induced differences in growth rate of juvenile herring during the first year of life appear to determine differences in size attained by a cohort at least to age 2. Growth appears to be related to both abundance at age 2 and summer water temperature, but, when abundance is high, 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 (to age 2) off western Maine than off eastern Maine. They noted that the western Maine area was characterized by higher zooplankton densities in summer, higher mean water temperatures and lower salinities than the eastern Maine area, and that growth of juvenile herring was consistently slower in eastern Maine. It is likely that the higher growth rate of herring off western Maine was due to higher temperature and/or greater productivity of zooplankton.

Sinclair *et al.* (1982) analyzed summer growth of juvenile herring from the southwestern 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. Incorporation of this change into the regression analysis gave results which are not inconsistent with density-dependent growth.

Grosslein *et al.* (1980) reviewed all available data on the diets of 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, were mackerel, alewife and sand lance. Of these, mackerel and sand lance were the only species which were suffi-

ciently abundant to have been potentially significant competitors of herring. The mackerel stock increased in the late 1960's while the herring stocks declined rapidly, but both stocks declined thereafter to low levels during the 1970's. At the onset of the population "explosion" of sand lance in the mid-1970's (Sherman *et al.*, 1981), the Georges Bank herring stock had already collapsed. Virtually all other fish species declined, along with herring, during the late 1960's and first half of the 1970's. Therefore, competition seems unlikely to have caused the decline in herring abundance.

Available information on predators of herring on Georges Bank was also summarized by Grosslein *et al.* (1980). Occurrence of herring and/or unidentified clupeoids was recorded in the stomachs of many fish predators from Georges Bank, with highest frequency in Atlantic cod, spiny dogfish, red hake, pollock and white hake. However, predation by the demersal fish stocks could not have caused the decline in herring stocks, because the predator stocks declined rapidly during the same period. Excluding mackerel and herring, the total finfish biomass on Georges Bank declined 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), but the herring stock had essentially collapsed when squid (*Illex*) abundance increased substantially in 1976 over previous levels.

As noted above, there has been much speculation about the possible interspecific interactions between mackerel and herring, but there is little direct evidence for rigorous evaluation of hypotheses. Anthony and Fogarty (1985) observed that there was a similarity between their results and those of Skud (1982) in the statistical relationships between temperature and herring recruitment and possible interactions with mackerel. Skud (1982) examined the historical mackerel and herring catch statistics which date 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 than herring or when shifts in the populations occurred. The same pattern was observed in the analysis of Anthony and Fogarty (1985) who found an inverse relationship between herring recruitment and water temperature during the recent period (1965-81) 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 herring abundance and temperature. Despite the intriguing correspondence of the two data series, they could not offer a specific biological rationale to explain such a relationship. Since changes in availability could not be distinguished from changes in

abundance in the early catch data, little more than speculation seems warranted.

Other important herring predators include marine mammals and large pelagic fishes (sharks, tunas, billfishes). All of these concentrate to feed on schooling fishes such as herring. Sissenwine *et al.* (1984b) speculated that marine mammals alone could have contributed to the collapse of the Georges Bank herring stock. They noted that the estimated biomass of marine mammals within the geographic range of the Georges Bank herring stock was sufficient to have consumed the entire population of herring that was estimated to have remained after the last commercial harvest in 1977. Their estimate did not include the possible predation by other apex predators whose fish consumption was estimated to be roughly 25-33% of the quantity consumed by marine mammals (Sissenwine, 1984; Cohen and Grosslein, 1987). It is possible that predators such as these can locate the dwindling schools of declining prey populations with rather high efficiency (much as fishing fleets do) and thus actually increase predation mortality for a given biomass of predators. This would be an example of a depensatory effect, as described by Sissenwine (1984).

Occasionally, disease has been responsible for drastic declines of herring populations in the Northwest Atlantic. 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 epizootic during the decline and collapse of the Georges Bank herring stock.

Process-oriented studies of herring recruitment

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 that control 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 basis of a very general hypothesis that year-class size is determined within the first year of life (ICNAF, 1975, p. 91). Most scientists that were involved in the program believed that the distribution, abundance and condition (size, robustness) of herring larvae after 6 months and the factors controlling these events might well provide clues to the causes of recruitment variability. However, there was clear recognition that additional sampling of postlarval stages was also needed, especially at the time of metamorphosis in the spring (April-

May), but the necessary resources were not available to implement this phase of sampling. In any case, the collapse of the stock after only 2–3 years of more intensive larval studies precluded the development of a time series sufficient for testing any hypotheses about effects of larval ecology on recruitment other than the relationship between initial larval production and recruitment. Accurate estimates of the strength of recruiting year-classes on Georges Bank after that of the 1970 year-class were not available, but it is apparent that they were very weak relative to the 1970 year-class (Anthony and Waring, 1980). In the other Gulf of Maine stocks, the 1971–76 year-classes were all relatively weak except for the strong 1976 year-class (Fogarty and Clark, MS 1983). Because the last spawning on Georges Bank to produce a significant number of larvae was in 1976, it seems that only one of the 6 years of larval data might have been characteristic of conditions conducive to good recruitment (assuming that the earlier regional coherence among year-classes would have continued and that the 1976 year-class would have been a strong one on Georges Bank under normal conditions). This does not provide much of a basis for evaluating the possible significance of factors such as growth rate and overwinter mortality, because the hypotheses involving these factors cannot be proved or disproved. Nevertheless, some important features of the ecology of herring larvae (<6 months old) on Georges Bank have been documented and these are summarized in the next section.

Larval growth, feeding and condition relative to mortality and environmental factors

Lough *et al.* (1982) fitted a Gompertz growth curve to data for a sample (311) of herring larvae from the Georges Bank–Nantucket Shoals and coastal Gulf of Maine areas, utilizing daily growth increments in otoliths. Average growth rates 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 0.20 mm/day, which is similar to average seasonal values from most other studies of larval herring growth. They noted that this agrees closely with estimated growth rates for Georges Bank–Nantucket Shoals herring larvae from modal analysis of length frequencies of the 1971–78 samples, which yielded an average of 0.195 mm/day for 7–30 mm size-classes over 163 days (Lough *et al.*, MS 1979). The form of the larval growth curve for Georges Bank appears similar to those for other herring stocks, with a slowing of growth in the mid-larval stage and a rapid increase at the time of metamorphosis.

Cohen and Lough (1983) investigated the relation between survival of larval herring and their feeding (gut analysis of more than 8,000 larvae), morphological

condition, and the distribution and abundance of their prey during the first 6 months of life, based on collections of larvae in the Georges Bank–Nantucket Shoals area during the 1974, 1975 and 1976 spawning seasons. In these years, there were differences in production, growth and mortality of larvae, as well as in spawning locations, and data were available on zooplankton prey and other environmental factors. Herring larvae fed on the dominant species of copepods (*Centropages* sp., *Pseudocalanus* sp. and *Paracalanus parva*) which were the same for the entire Georges Bank–Nantucket Shoals area. The larvae consumed much lower numbers of *Centropages* sp. in 1975 and 1976 than in 1974, and this was associated with a change in distribution and abundance of prey species 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 relative to the same periods in other years. *Paracalanus parva* was very scarce in February 1976 but was widespread, although low in numbers, during February 1975.

Both the growth and survival rates of herring larvae increased over the autumn-winter periods following spawning in 1974–76, coincident with declining abundance of larvae and shift of spawning area from eastern Georges Bank to Nantucket Shoals. The estimated age-specific mortality rates (Lough *et al.*, 1981) showed that mortality was lowest in 1976 (2.2% per day), higher in 1975 (2.7% per day) and highest in 1974 (3.2% per day), whereas larval production was highest in 1974 (79×10^{12} larvae), lower in 1975 (21×10^{12} larvae) and lowest in 1975 (1×10^{12} larvae). Mean length of larvae increased during each succeeding winter over the 3 years, indicating that larval growth was increasing or that larger larvae were surviving in greater numbers. In addition, a higher percentage of feeding larvae was found in the 1976 season, although their stomachs contained fewer prey of smaller sizes and lower biomass of prey per larva (Cohen and Lough, 1983). The larvae that were collected in the 1976 season appeared to be more robust for their size, based on a condition factor index. Thus, trends of increasing growth and overwinter survival appeared to have been 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 in the Georges Bank–Nantucket Shoals area were extremely low, relative to estimated prey densities that are required for good growth in herring larvae from other studies. Average temperatures (0–50 m) in the Georges Bank–Nantucket Shoals area were quite similar in the 3 years (10° to 11° C in December and 6° C in February), with slightly higher values in the 1974 season when larval abundance was highest and the growth and survival rates were lowest.

Temperature, transport and other factors

A shift in the timing and location of herring spawning occurred during the 1970's. The onset of spawning (hatching) season occurred progressively later during the 1971-77 period, ranging from mid-September to mid-October in 1971-73 to late October-early November in the later years (Lough *et al.*, 1981). The delayed spawning may have been related to (a) the shift of major spawning from northeastern Georges Bank to the western part of the Bank and Nantucket Shoals where spawning is normally 1-2 weeks later, (b) the decline in number of larger (older) fish which tend to spawn earlier, and (c) the general increase in autumn bottom temperatures (Lough *et al.*, 1981).

The trend toward later spawning has not been linked to changes in larval survival, but it has been suggested that temperatures on Georges Bank may have become high enough to impair egg development and reduce larval survival. Grimm (1983) examined near-bottom temperature data in relation to spawning areas delineated by distribution and abundance of newly-hatched larvae (≤ 8 mm SL) and noted that mean temperatures in these areas 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 ($>13^{\circ}$ C) on Georges Bank during October since 1971, hatching success may have been reduced. He noted Blaxter's (1956) observation that hatching success tends to decline at temperatures above 12° C. He also noted the studies by Alderdice and Velsen (1971) which showed mortality of Pacific herring (*Clupea palassi*) within 4 days after hatching at temperatures about 13° C. Grimm (1983) noted that high temperatures ($>16^{\circ}$ C) on Georges Bank were recorded at the beginning of the spawning seasons in 1971-74, and that these high temperatures could have had a deleterious effect on egg and larval survival and may have contributed to the shift of spawning activity from Georges Bank to Nantucket Shoals. Autumn bottom temperatures on Nantucket Shoals are normally lower than those on Georges Bank, and this was particularly the case in 1976 and 1977 when spawning occurred principally on Nantucket Shoals.

Although the possible deleterious effect of high temperatures on survival of larvae cannot be ruled out, there is no clear evidence to support this hypothesis. In fact, growth of larvae during the 1971-78 seasons appeared to be within the normal range (Lough *et al.*, MS 1979). Furthermore, the correlation between larval abundance and spawning stock size (Lough *et al.*, 1985) would probably not have been evident if unusually large and variable mortality had taken place during the egg and early larval stages.

Water circulation on Georges Bank is characterized by a clockwise mean residual flow around the crest

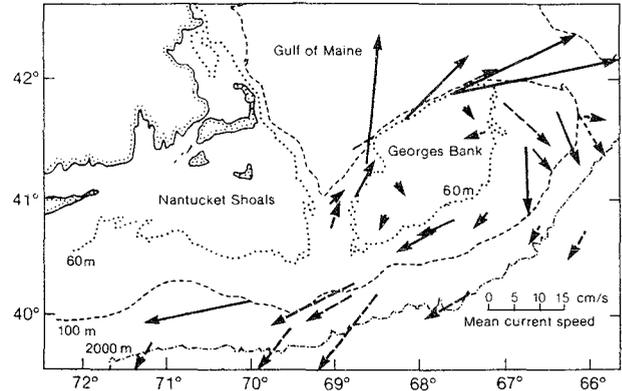


Fig. 10. Mean circulation pattern on Georges Bank, based on satellite-tracked drifters with drogues at depth of 10 m. Speed of current is represented by length of arrow from measurements in December 1978 (long dash), March 1979 (short dash) and August 1979 (solid line). (Adapted from Butman *et al.*, 1982.)

of the bank (<60 m) which has been postulated 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 the bank, southeastward and southerly components on the eastern edge, and southerly and southwestward components on the southern flank (Fig. 10). Although the gyre is a persistent feature throughout the year, being generally stronger in summer than in winter, it is subject to periodic disruptions and variations in current speed in relation to events such as storms and warm-core rings.

Lough *et al.* (1985) summarized the average pattern of larval herring dispersal from the spawning areas on Georges Bank and Nantucket Shoals and showed that larvae disperse rapidly over the shoal areas and reach the maximal extent of their distributions by late November or early December (Fig. 3). During late autumn and winter, 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 northeastern Georges Bank typically disperse to the southwest across the bank at 2-15 km/day and intermix with larvae from Nantucket Shoals. Large larvae are sometimes found in lobes extending off the northern edge of Georges Bank 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 the cross-transport of herring larvae between Georges Bank and Browns Bank on the Scotian Shelf or between Nantucket Shoals and western Gulf of Maine coastal waters, at least during the first 6 months.

Bolz and Lough (1984), utilizing data from the 1971–77 larval herring surveys, analyzed the composition of ichthyoplankton communities on Georges Bank in relation to water mass properties (T/S distributions) and showed that there were two groups: a northern group (shelf spawners) in the cooler, less saline shelf water, and a southern group (mesopelagic and subtropical) in the 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 seasonal variations in the southern faunal zone, 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 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. Strong persistent northerly winds, as occurred during November, January and February of the 1976/77 season, tended to shift the shelf-slope frontal zone 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 temperature and salinity characteristics of Gulf of Maine water (Wright, 1979) and also by 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 1976/77 season, 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, there is probably significant disruption of the clockwise flow which serves as a retention mechanism for larvae spawned on Georges 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 water with possible effects on recruitment.

With respect to larval herring, however, there is no direct evidence of significant advective loss south of Georges Bank, because the ICNAF larval herring surveys rarely extended even to the shelf-slope frontal zone. Also, despite the occasional occurrence of large larvae just north and east of Georges Bank (noted above), there was minimal evidence of significant northward or eastward transport off the bank (Lough *et al.*, 1985). In addition to the stormy winter of 1976/77, the two following winters of 1977/78 and 1978/79 were also characterized by unusually strong northerly and northwesterly winds and record low temperatures (Ingham, 1982). Advective loss of herring larvae from the Georges Bank–Nantucket Shoals area 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 than usual on Nantucket Shoals) in those years had already operated prior to the severe winter seasons. Thus, there is no clear evidence to indicate that advective loss of larvae was a major factor in the decline of the Georges Bank herring stock.

Dispersal from the spawning sites was discussed by Sinclair and Iles (1985) in relation to their two hypotheses for explaining 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 were 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 waters off western Nova Scotia, on Georges Bank, on Nantucket Shoals, and in coastal Gulf of Maine. In the hypothesis of Sinclair and Tremblay (1984), the timing of spawning in each of these areas was postulated to be a function of the time necessary to complete the larval phase and yet metamorphose within the April–October period. Autumn spawnig populations in well-mixed waters are adapted to conditions of slow larval development through the winter period of low temperatures and low food density, whereas spring-spawning populations produce larvae in stratified waters with higher temperatures and higher food density, which enable the larvae to complete the same amount of development to metamorphosis within the same “window of time”. With respect to dispersal of larvae and postlarvae, Sinclair and Iles (1985) concluded that migration to the juvenile nursery areas occurs subsequent to metamorphosis rather than during larval drift. They noted that the northeastward drift of larvae off western Nova Scotia 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 their slower dispersal, similar to inferences drawn from estuarine studies that vertical migration of larvae in relation to tidal cycles is the retention mechanism in those situations (Graham, 1972).

In preliminary studies of vertical distribution of herring larvae on Nantucket Shoals in 1977, Potter and Lough (MS 1980) showed that herring larvae did migrate vertically but not in a consistent pattern. In one 24-hr series, larvae were concentrated in the surface layer during both day and night hauls, but, in another 24-hr series (apparently on the same group of 5–30 mm larvae), the larvae were distributed uniformly throughout the water column during both day and night. In both series, the mean length of larvae increased with depth. Unpublished data on vertical distribution of larvae off Cape Cod have also shown wide distribution throughout the water column and a tendency for the larger larvae to be deeper (R. G. Lough, Northeast Fisheries Center, Woods Hole, Mass., pers. comm.).

Sinclair and Iles (1985) concluded that maintenance of an aggregated larval population may be essential for the successful establishment (and presumably persistence) of a spawning stock. Larvae that are lost from the aggregate (i.e. are dispersed so widely that density decreases below some critical level) may not be able to recruit to the migrating populations subsequent to metamorphosis. Although the authors did not suggest a 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 dispersal chiefly during the late larval stage. If this is the case, variations in circulation could exert control over recruitment success. However, there is no evidence to support or disprove such a link with circulation.

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