International Commission for the Northwest Atlantic Fisheries

Serial No. 3586
(D.c.9)

ICNAF Res.Doc. 75/100

ANNUAL MEETING - JUNE 1975

A conceptual model of stocks of herring (*Clupea harengus*) in the Gulf of Maine

by

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Introduction

Up to 1960 the herring fisheries off New England and Southeastern Canada consisted largely of the "sardine" fishery for immature two-year old herring with exploitation of one-year old "brit" for pearl essence, fish meal and lobster bait. Some older fish were also taken for fish meal and lobster bait and some for pickling, particularly in Nova Scotia.

These fisheries remained quite stable with only an occasional poor year. The adult stock on Georges Bank (ICNAF Subarea 5Z) was virtually unexploited except for some small contribution during winter and spring to trap fisheries in New Jersey and to the Southern New England industrial fisheries while the adult stock in ICNAF Subarea 5Y was subjected to limited exploitation for lobster bait and fish meal.

In 1961 the Soviet distant water fleet began to exploit the Georges Bank stock and they were soon joined by distant water fleets from other countries. These fisheries expanded southward on overwintering fish and into the Gulf of Maine. At about the same time, the failure of the Pacific herring fishery of British Columbia led to the diversion of efficient purse seiners from the west to east coasts of Canada. Demand for fish meal was increasing and the exploitation of adult herring stocks in the Gulf of St. Lawrence, off Newfoundland, off Nova Scotia, off the Western Gulf of Maine Coast, and on Georges Bank increased dramatically from 180 thousand metric tons in 1960 to a peak of 967 thousand metric tons in 1969 (Table 1).

In 1964 there began a series of serious failures in the Maine herring fisheries. The history of the fisheries indicates that after two excellent year classes in 1960 and 1961 there occurred a series of poor year classes in 1962, 1963, 1964, and 1965; the 1966 year class was a moderately good one followed by poor year classes in 1967, 1968 and 1969. The first really good year class in the area in nearly a decade occurred in 1970.

Despite considerable research effort, we still have a poor understanding of the causes of this decade of poor recruitment. The economic and social importance of this problem was further magnified by a nearly worldwide failure of recruitment to herring stocks with particularly disastrous failures in the Northeast Atlantic herring stocks. This has led to increasing pressure on the remnants of the Northwest Atlantic herring stocks by distant water fleets from European countries for whom herring is a staple dietary element. Vigorous efforts have had to be made in ICNAF to develop management regimes that will prevent pressures on the Northwest Atlantic herring fisheries that will lead to their irreversible depletion.

The purpose of this conceptual model is to provide a framework of hypotheses and present understanding against which alternative hypotheses and research activities can be forged and developed. The major elements will concern ecology and recruitment. Population dynamics studies on the stocks have been adequately developed by Anthony (1972), Schumacker and Dornheim (1971), Schumacker and Anthony (1972), Anthony and Brown (1972), and Miller and Halliday (1974) for the stocks in ICNAF Subareas 5Y, 5Z, and Statistical Area 6 and 4XWb, considering our present ecological knowledge, and will only briefly be touched upon in this document.

Larkin (1972) has indicated in a provocative essay that development of models and simulation modeling are needed in fishery management "to explore the widest spectrum of consequences of the widest range of alternative policies." Larkin also points out two shortcomings in present modeling work:

"First is the danger that the models will be believed..." (In the present case there is sufficient diversity of opinion among fishery biologists and managers concerned with herring to minimize this danger.) The second shortcoming that Larkin sees is "that most model schemes are painfully unimaginative, largely dealing with exhaustive but trivial extrapolations of a set of assumptions that are already passé." My efforts may suffer from this shortcoming; nevertheless, they will hopefully provide a basis for hypothesis development and simulation modeling that are needed for the development of better management strategies.

Patten (1971) has stated:

> Modeling spans a spectrum from *isomorphic* formulations in which components and interactions of systems are captured on a one-to-one basis, to *homomorphic* representations where details are collapsed many-to-one into lumped variables and parameters. The former emphasize realism and detail while the latter grade into abstraction and generality. The trick of effective modeling is to somehow strike a balance between the two extremes that is appropriate for what should be explicitly defined goals and objectives.

To attempt to strike some such balance, my approach will be to discuss all factors that I feel might influence herring production systems. From this discussion I will develop specific premises and hypotheses concerning those factors and interactions which I consider most important or critical to the herring production systems under consideration. My specific goal is to synthesize present knowledge of stocks in the area, my best guesses based on present understanding of herring stocks in other areas, and outright hypotheses, into a unified conceptual model that can be used to guide the planning and design of research efforts, as background for development of alternative hypotheses, and to serve as a preliminary heuristic model for prediction and simulation. Such prediction and simulation hopefully would be useful in examining the consequences of various research and management strategies. To develop a more simple, homomorphic, and thus tractable model, I will select those factors which I believe are most critical to the herring production system. I will finally discuss some mathematical approaches that I think would be useful for simulation and analysis of this system.

Table 1. Total US and Northwest Atlantic herring catches, 1960-1973.

	TOTAL U.S. CATCH 1000 METRIC TONS	TOTAL NW ATLANTIC CATCH 1000 METRIC TONS
1960	70	182
1961	26	182
1962	72	344
1963	70	285
1964	28	304
1965	34	264
1966	33.6	432
1967	33	594
1968	42	952
1969	32	967
1970	31	852
1971	35	747
1972	41	549
1973	26.3	486

Distribution

General distribution and stock structure

1. Observed distribution. In the Western North Atlantic, the sea herring (*Clupea harengus*) occur from Cape Hatteras to the Arctic Circle in Western Greenland. In this model I will consider only those stocks occurring in ICNAF Subareas 4XW, 5Y, 5Z, and Statistical Area 6 (Figure 1). Interactions of stocks in these areas with Gulf of St. Lawrence-Newfoundland stocks are believed to be minimal and for the purposes of this report will be ignored.

Within the areas under consideration there are three major stocks or stock-complexes. Starting in the northeast, the first is the Southern Nova Scotian stock with the major spawning areas being Trinity Ledge and Lurcher Shoals. Additional minor spawning of this complex occurs on the western side of Passamaquoddy Bay, on Grand Manan Banks, and at several areas along the Nova Scotian shore from St. Mary's Bay to Halifax.

The second is the Southwestern Gulf of Maine stock with the major spawning area being the southwestern section of Jeffreys Ledge. Additional spawning areas within this complex are Stellwagen Bank, Isle of Shoals, off Cape Elizabeth, Maine, and several small areas along the Maine coast.

The third stock is the Georges Bank stock. Major spawning areas are the northern edge of Georges Bank and Nantucket Shoals. There is some evidence of minor spawning in the southeastern part of Georges Bank and on the east side of Great South Channel.

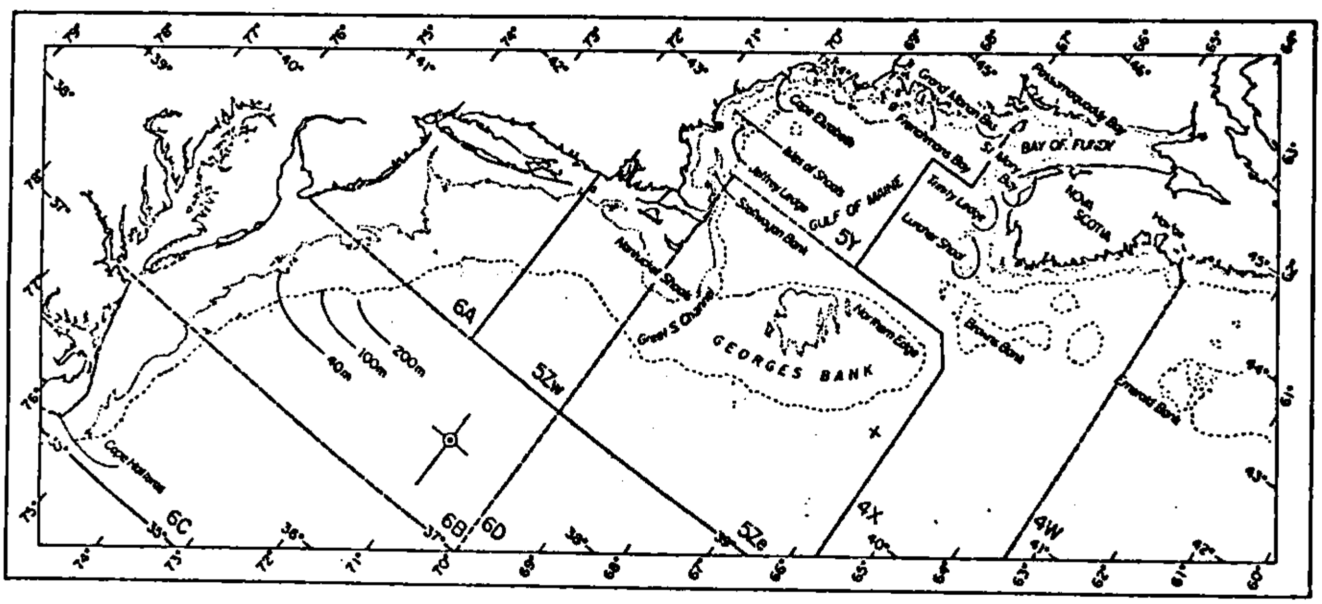


Figure 1. Location of areas mentioned in this report.

2. Physical determinants of distribution. Physical factors, in their interaction with physiological requirements and behavior of herring, play major roles in determining the distribution of the species. These include temperature, salinity, currents, and depth. Temperature is one of the major determinants of distribution. Herring prefer temperatures in the range of 8 to 12° C (Stickney, 1969). Physiological stress is induced below 4° C and above 16° C while temperatures below 0° C and above 20° C are lethal (Brown, 1960*a*). (Exact lethal points are dependent on other factors including oxygen concentration, salinity, and prior conditioning.) In general, herring are creatures of the shoaler portions of the shelf. They prefer waters of 28 to 32 parts per thousand salinity (salinity as low as 5‰ can be tolerated - Brown, 1960*b*), and depths of less than 100 meters. Post larvae and juveniles tend to concentrate in shoal inshore areas, particularly in summer and fall, while adults may undertake seasonal

migrations that take them into waters as deep as 100 to 200 meters. Oceanic currents are also major physical determinants of herring distribution. They play an essential role in dispersing the larvae over suitable nursery grounds.

The general behavior of post larvae, juveniles, and adults is to swim against a current during daylight hours when the bottom can serve as a visual reference.

3. Biotic determinants of distribution. There are two major biotic factors which influence herring distribution. These are, first, the necessity for herring to seek out their zooplankton food organisms. Thus, in order for herring to survive, their distribution must overlap that of their zooplankton prey. Despite this, attempts to directly correlate herring distribution and abundance with zooplankton distribution and abundance have met with varying success, indicating complex interactions with other factors (Blaxter and Holliday, 1963; Lie, 1961).

The second biotic influence on herring distribution is the occurrence of phytoplankton. Herring avoid dense concentrations of phytoplankton, particularly concentrations of *Phaeocystis* (Lie, 1961).

4. Discreteness of stocks in the area. Although there is certainly interaction among the three stocks outlined in section 1, above, and the boundaries between them have been somewhat arbitrarily selected, the major stocks are discrete self-perpetrating units. By this, I mean that recruitment from one spawning stock to another is negligible and that it is highly unlikely that progeny from Georges Bank spawning would themselves spawn in any area other than Georges Bank. If there were significant random mixture among the stocks, differences among them in age composition, fecundity (Perkins and Anthony, 1969), and parasite fauna (Boyar and Perkins, 1971) ceuld hardly be maintained. The mechanisms whereby and the degree to which these stocks maintain themselves as discrete units are of general biological interest and of importance to the development of optimal management strategy.

There is considerable evidence that herring stocks in other areas return as adults to the area where they were spawned (Harden-Jones, 1968; Zijlstra, 1963; Iles, 1965). I believe that herring stocks are genetically and physiologically adapted to the area in which they are born, successfully survive and reproduce. Such adaptation must require fairly consistent oceanographic regimes that maintain the stocks separated throughout their life, or at least until they have found their own spawning area once. Precise mechanisms for segregation and homing would be required if the stocks intermingle as juveniles in inshore waters, during overwintering, or during spring and summer feeding migrations before they have found their natal area and learned the way back to it.

Homing mechanisms comparable to those demonstrated for salmon (where memory of the characteristic "smell" of natal waters is imprinted during early development, recognized some distance out in the open sea, and followed "upstream" to the river mouth and further to the tributary of origin) are difficult to postulate to account for return of herring to the same spawning grounds in the open ocean where they were hatched and from which they and their cohorts were dispersed as larvae. Such difficulties and the available evidence lead me to the conclusion that the stocks remain largely separate through at least the juvenile stage.

I postulate three mechanisms for the maintenance of separate stocks. The major mechanism is related to larval dispersal. Each of the stocks is dispersed by ocean currents from the spawning area to its own separate nursery area. These current systems, which will be discussed in more detail in the section below on larval distribution, also tend to maintain the larvae through the early weeks and perhaps months of their life in these shoal nursery areas in reasonably close proximity to their spawning area. Return to the spawning area would be accomplished by contranatal migration (Harden-Jones, 1968). Those larvae which are not maintained within their own system probably would not survive the drift over deep waters separating them from other nursery grounds.

The physiological and genetic adaptation to the oceanographic regime within their own territory not only results from separation but tends to reinforce it. Those individuals that are transported out of, or stray from their home territory, particularly during early life stages, would be less adapted to the "foreign" area and thus less likely to survive and reproduce within it. Thus, adaptation to home territory is a second mechanism tending to maintain separate stocks.

The third mechanism maintaining separate stocks is related to the schooling behavior of herring. Instead of individuals randomly dispersing throughout the total area, directive behavioral tendencies, *e.g.*, contranatal migration, which may be weak in individuals, are reinforced and summed throughout the school. Such schools would search out spawning sites within their own home territory by locating the proper depth zone along the edges of their shoal habitat and follow the depth contour until a suitable site for spawning was located.

5. Interrelationships among the three stocks in the area. Despite the discreteness of the three stocks or stock-complexes under consideration, there are certain interrelationships or interactions among them that need to be kept in mind. First, although the amount of straying and genetic interchange among the stocks is restricted, the frequencies of several variable genes are remarkably close (Ridgway, Lewis, and Sherburne, 1971; Lewis and Ridgway, 1972; Odense, Leung, and Amand, 1973), implying that there is some exchange of genes among them. For the purposes of this model, the amount of exchange between the stocks is considered to be so small as to not significantly affect recruitment over a decade or more.

Second, during their first and second years of life, the Nova Scotian stock and Southwestern Gulf of Maine stock intermingle along the coast of Maine and in the Bay of Fundy. Thus, there is some competitive interaction between these two stocks and some sharing of fishing pressure in the juvenile fisheries.

Third, patterns of adult migration indicate that some elements of the Southwestern Gulf of Maine stock share overwintering areas in the Mid-Atlantic Bight with the Georges Bank stock resulting in some possibilities for competitive interaction.

The fourth interrelationship among the stocks is more apparent than real. There are strong correlations between good and poor year classes among the three stocks but this is readily explained since major aspects of oceanic climate are similar in the areas where the three stocks spawn and spend their lives. This relationship has a positive advantage for prediction and management; recruitment indices developed for one stock can be applied with some accuracy to all three (Anthony, 1972).

Requirements for spawning and hatching

Atlantic herring are benthic spawners that attach their eggs to the bottom substrate. Consequently, this species has some special requirements for adequate spawning sites. These requirements are:

1. Nature of bottom. Gravel is the preferred type but sand, cobble, and attached algae are also used.

2. Depth. Although some spawning in shallow water has been noted, and a few cases of spawning to depths of 200 fathoms are known, herring in the Western Atlantic generally spawn at depths of 20 to 50 fathoms.

3. Temperature. Bottom temperatures between 5^{o} and 12^{o} C are required for spawning and incubation. Although there are reports that herring will hatch normally from 1^{o} to 22^{o} C, the optimal temperature for development is known to vary with different races. The temperature for spawning in the stocks under consideration in this model are generally confined to a much narrower range, about 5^{o} to 12^{o}. Optimum survival occurs at 8^{o} to 10^{o} C. Lower temperatures prolong incubation and exposure to predation; higher temperatures subject the eggs to danger of bacterial and fungal attack, while temperatures above 16^{o} C result in abnormal physiological development.

4. Currents. Major spawning sites are flushed by strong tidal currents which provide aeration of the incubating eggs. Once the larvae hatch out, the prevailing currents characteristically disperse the larvae over suitable shallow nursery grounds and retain them there (until they develop adequate swimming capacity to seek out suitable niches for themselves) rather than sweep them out into hostile deep ocean waters. I postulate that variation in this dispersal/retention mechanism is a major cause for variations in year-class strength. This mechanism will be discussed in detail for each of the major spawning sites below.

Distribution and dispersal of larvae

1. Distribution and dispersal of individual stocks. The distribution and dispersal of herring larvae within the area of interest has been extensively studied. The results of the studies up to 1970, particularly those for offshore areas, have been assembled and reviewed by Boyar, *et al.* (1973). Studies on the distribution of herring larvae in inshore waters of the Western Gulf of Maine were reported by Graham, Chenowith, and Davis (1972), and recent studies on their distribution in the Bay of Fundy and Southern Nova Scotian waters were reported by Iles (1971), Tibbo (1968), Messieh, Tibbo, and Lauzier (1971), and Sameoto (1972). More extensive studies were started in the fall of 1971 with cooperative ICNAF surveys using standardized methods and sampling grids. The data have been summarized in ICNAF documents (Ridgway *et al.*, ICNAF Res. Doc. 72/123; Schnack and Stobo, ICNAF Res. Doc. 73/115; Schnack, ICNAF Res. Doc. 74/105). These cooperative surveys combined with the earlier studies allow a quite

detailed understanding of most of the aspects of larval distribution and ecology. Unfortunately, the coverage of the Bay of Fundy and Eastern Nova Scotian areas was not carried out as planned in the three years, and the inshore Western Gulf of Maine sampling was not conducted in 1973.

Although detailed analysis of the data is yet to be carried out, the major conclusions from the joint surveys are that the larvae from each spawning area are quite consistently dispersed onto shoal nursery grounds and that drift between the three major areas is limited. The dispersal patterns found may be summarized as follows.

From the spawning grounds off Southwest Nova Scotia, the major larval drift is into the Bay of Fundy. Some drift across the mouth of the Bay of Fundy and mixture with larvae from Grand Manan Bank spawning seems likely, particularly from Canadian studies in 1969 and 1970 (Messieh, Tibbo and Lauzier, 1971). The larvae from spawning on Grand Manan Bank (and off Cutler, Maine) drift southwestward along the Eastern Maine shores as far as Frenchmans Bay. Larvae from spawning along the Southeastern Nova Scotian coast remain in the area throughout the fall and winter (Sameoto 1972).

Larvae from the Southwestern Gulf of Maine - Jeffreys Ledge spawning groups drift shoreward into shallow bays and estuaries. Of particular interest is the finding that larvae from Jeffreys Ledge spawning are dispersed shoreward apparently by the clockwise gyre in the area (Graham 1970). Only a minor portion of the larvae was found on the seaward side of the ledge in a detailed study conducted in 1972 (Boyar *et al.* 1973).

Larvae from the spawning on the northern edge of Georges Bank disperse southwestward over the banks. The divergence at the northern edge apparently prevents dispersion northward and mixture with Nova Scotia spawned larvae as has been postulated by some authors. Along the southern edge of Georges Bank the dispersal is quite consistently westward with only occasional larvae found drifting into the deep waters south of the Bank. The westward drift of Georges Bank larvae mixes them to some extent with larvae from spawning on Nantucket Shoals.

Dispersal of Nantucket Shoals spawning appears to occur in two directions; southwestward on the southern New England shelf and northeastward onto Georges Bank, indicating further mixing. Some spawning occurs on the east side of the channel with draft eastward onto Georges Bank. The mixture of larvae between Georges Bank and Nantucket Shoals is indicative that herring spawning in the two areas are members of the same stock. Time of spawning in Nantucket Shoals usually occurs later than that on Georges Bank but this varies from year to year. The relative magnitude of larval production between spawning on Nantucket Shoals and Georges Bank is also remarkably variable. The ratio of estimated production between the two areas varied from twelve to one in favor of Georges Bank in 1971 to four to one in favor of Nantucket Shoals in 1972 to 1.5 to 1 in favor of Georges Bank in 1973 (Schnack, ICNAF Res. Doc. 74/105).

2. Vertical distribution. The vertical distribution of larvae is an important aspect of their ecology and behavior and is especially important to designing adequate sampling methods particularly since diurnal changes in distribution also interact with avoidance of sampling gear during daylight hours. Observations by divers (Cooper 1975 ICNAF Res. Doc.) and from submersibles (Graham and Chenoweth 1973) indicate that newly hatched larvae spend one or more days near the sea bed. Observations on vertical distribution of herring larvae have been made by Bridger (1958), Colton *et al.* (1961), Wood (1971), Schnack and Hemple (1971). These studies indicate that larvae are not homogeneously distributed over the whole water column. Small larvae (after the first few days) are more abundant in the upper layer and less abundant close to the sea bed. Larger larvae are homogeneously distributed at night but during the day they avoid the upper layers. Catches of larger larvae were more abundant at night indicating avoidance of the net in daylight. The results are not completely consistent among these studies indicating interactions among light level, size and depth.

3. Larval Survival. The importance of dispersal mechanisms and their interactions with other critical aspects of larval ecology.

The nature and consistency of mechanisms whereby larvae are dispersed from their spawning grounds are undoubtedly critical aspects of the ways in which the environment interacts with spawning stock abundance to determine the size of a year class. The species and their component stocks have adapted to secular and spatial environmental variability in two major ways; high fecundity and the timing and locale of spawning. High fecundity provides the plasticity necessary for survival of the stock despite wide environmental variations. It also provides the opportunity for the occasional survival of very large year classes when environmental factors are more favorable than normal. The relative consistency in timing and location of spawning indicate that the stocks have evolved physiological and behavioral patterns which insure that they spawn in the times and places that provide the most consistent and ideal mechanisms of dispersal for larval survival. Of course, a certain amount of diversity in time and place of spawning is important to provide additional resistance to environmental variation.

In each of the spawning areas the pattern of dispersal is quite consistent in dispersing the larvae over shallow nursery grounds. In some cases the dispersing and containing mechanisms are subject to variation during the first few weeks when the larvae are completely at the mercy of ocean currents. If the current system over Georges Bank, which consists of a clockwise gyre with a divergence on the north and westward outflow along the shelf, breaks down, a significant portion of the larvae is lost into the deep waters to the north, or more disastrously, significant quantities of the larvae containing shelf waters become entrained in slope waters to the south, transporting the larvae into not only deep water but areas where the water temperature will quickly rise above their lethal limit. An example of this phenomenon was observed in the spring of 1956 (Colton, 1959). The extension of tongues of warm slope water onto Georges Bank has been observed several times in recent years. Walford (1938) pointed out the importance of the relatively stable eddy on Georges Bank to the survival of the haddock stock in the area. On the other hand, the seeming instability of this system caused Colton and Temple (1961) to consider spawning on Georges Bank an enigma. Bumpus (1974) has recently reviewed our knowledge of ocean circulation on the continental shelf of the east coast of the United States. Included in his review is additional and more complete treatment of this phenomenon.

Breakdowns in the circulation system that disperses herring larvae from Nova Scotian spawning into the Bay of Fundy, or that disperse Jeffreys Ledge larvae into shoal waters of the western Gulf of Maine coast, also have significant adverse effects on survival of year classes of these stocks.

The importance of ocean currents as dispersal and retention mechanisms significantly affecting survival of herring has also been pointed out for Pacific herring by Stevenson (1962).

There are a number of other interactions between the environment and larval ecology that must have significant effects on survival. The same mechanism that maintains larval herring on Georges Bank has been hypothesized to maintain the population of *Sagitta elegans* (Clarke, Pierce, and Bumpus, 1943), one of the major predators of larval herring. Environmental variability also markedly influences the production of planktonic food organisms necessary for larval survival.

Distribution, migration, and behavior of post-larvae and young-of-the-year (Brit)

It is only after the larvae have undergone the enormous and highly variable mortality that occurs from spawning throughout the first winter that the size of a year class is stabilized and can be reasonably estimated. The end of the first winter is also a critical time for understanding the possible intermingling of stocks.

As the shoal waters cool with advancing winter, the aggregations of larval herring disperse into deeper, warmer waters. Winter storms break up the characteristic circulation patterns, further contributing to larval dispersal, and thus early in the spring herring larvae are found rather widely dispersed and in the deeper waters along the edge of the shelf. Nevertheless, the larvae are now strong swimmers and able to maintain their association with the territory of their own stock.

With the warming of spring, the larvae begin to aggregate and return to shoal areas. As the summer advances, the aggregations of young-of-the-year begin to undertake significant migrations. The coastal waters in the southwestern part of the Gulf of Maine become less and less suitable for herring, forcing northward migration.

A major habitat for young-of-the-year (YOY) herring is along the eastern Maine coast (Davis and Graham, 1970), and in the Bay of Fundy where enormous numbers used to be caught for production of "pearl essence" (crystalline guanine used in cosmetics and paint), and fish meal (Miller and Halliday, 1974). Here intermingling of southwestern Gulf of Maine and Nova Scotian stocks probably occurs. Young-of-the-year herring (2½ to 4 inches in length) have been found on Nantucket Shoals in mid-July (Bigelow and Schroeder, 1953). Since adequate shoal habitat is available on Georges Bank and Nantucket Shoals, I postulate that YOY herring of the Georges Bank-Nantucket Shoals stock remain in their home territory.

Distribution, migration, and behavior of juvenile herring

The major commercial fisheries for juvenile herring occur in the inshore waters of the Gulf of Maine and the Bay of Fundy in summer and in the fall. However, juvenile herring of age 2 and 3 have been found both by commercial fishermen and by scientific exploratory fishing (Smith, 1963) in winter somewhat further offshore along the western Gulf of Maine coast.

Some juveniles were found in shoal waters of Georges Bank in the early '60s using gill nets (Boyar, personal communication). The abundant 1970 year class was encountered in February and March of 1972 by the Soviet fishing fleet and Soviet research vessels off Cape Hatteras, on Nantucket Shoals, on Georges Bank, and on Browns and Emerald Banks. Thus, there is no longer any reason to believe that juveniles are confined to the Maine and New Brunswick and Nova Scotian coasts. As the spring and summer advances, those off southern New England probably move onto Nantucket Shoals, those on Georges Bank onto Cultivator and Georges Shoals, those on Emerald Bank into Nova Scotian waters. The juvenile herring off the eastern Massachusetts coast are forced to move northward by the warming temperatures as the season advances; others in the deeper waters off the Maine coast move inshore and northward as the season advances. Meristic studies (Iles, 1970; Anthony, 1972) indicate to me that juvenile herring from Jeffreys Ledge spawnings migrate as far north as the west side of the Bay of Fundy. (Some authors believe these fish are from the Georges Bank spawning; I see no necessity for drawing this conclusion and find it very difficult to formulate a mechanism for maintenance of discrete spawning stocks if this is the case.) In the late fall and winter the trend is reversed, with the southwestern Gulf of Maine herring moving southward and/or offshore as the shoal waters cool.

Distribution, behavior, and migration of adults

The distribution of adults is essentially the same as that outlined for juveniles except that they have less tendency to be associated with shoal or inshore waters, are thus more inclined toward diurnal vertical migration, they undoubtedly undertake more extensive feeding migrations with concomitantly greater possibilities for intermingling among stocks, and they of course undertake regular spawning migrations.

The Nova Scotian spawners overwinter in the Bay of Fundy and on the Scotian Shelf; recent Canadian tagging studies show they migrate as far north as Cape Breton (Stobo, Scott, and Hunt, 1975). They move into the nearshore waters of southern Nova Scotia in the summer and spawn on Lurcher Shoals, Trinity Ledge, Grand Manan Bank, and other nearby areas in the fall. Spawning starts in late August and extends through October. There is a small stock of herring spawning in the spring in Saint Marys Bay. This stock is negligible compared to the fall spawning stock in the area and has not been considered in this report. Fish of the southeastern Gulf of Maine herring stock overwinter in the deeper waters of the Gulf of Maine and in southern New England waters, where they intermingle with the Georges Bank stock. They spend the summer along the coast of Maine, and spawn in the fall on Jeffreys Ledge off Cape Elizabeth and in other minor areas. Spawning starts in late September or early October and extends into November.

The Georges Bank stock has been extensively observed by European fleets, research vessels from the USSR, Poland, and Germany, and by US research vessels (Boyar, 1968; Zinkevitch, 1967; etc.). Some fish overwinter on the bank, but most move off to the southwest overwintering from Nantucket Shoals to Cape Hatteras. In the spring they move northward, spend the summer on Georges Bank, and spawn on the northern edge and Nantucket Shoals in the fall and early winter. Spawning begins in late September and extends through the first half of December. Immediately after spawning, the adult fish move off the spawning grounds and begin their migration southwestward to the overwintering grounds.

Factors affecting the recruitment process of herring

There have been many attempts to relate a variety of factors to the level of recruitment in herring stocks. These can be divided roughly into three categories:

1. Spawning stock size.
2. Biotic environmental factors such as predator and prey density and availability.
3. Physical environmental factors such as temperature and currents.

The limited success of these studies is due to the complex operation of several factors with strong interactions on the recruitment process. Only an integrated study of the total system which takes into account the interactions among several critical factors will allow full development of a useful and predictive model for herring recruitment. When developed, such a model would undoubtedly be readily modified to describe and predict recruitment in other important species in the area.

Stock size and density dependence

1. Relationships between spawning stock size, fecundity, and recruitment. Although numerous studies have been made on stock recruitment relationships in herring (Hempel, 1963), regular relationships have been found for only a few stocks, and the relationships deduced from empirical data seem

to vary considerably between stocks. Cushing and Harris (1973) have fitted stock recruitment data on a number of Pacific and Atlantic herring stocks to a theoretical equation. The scatter of the data and the variations in the shape of the curves are quite remarkable. Two stocks within the North Sea, the Dogger and Buchan stocks, have quite different shaped curves. Such variability is generally conceded to be due to strong interactions among variable environmental factors and the high fecundity of the stock as they affect the recruitment process. Thus, to understand and predict recruitment in herring, understanding environmental influences is essential.

Cushing and Harris deduced from the stock recruitment relationships in herring that "there is danger that the stocks can be exploited to extinction." Most herring biologists would agree with Garrod's (1973) statement: "The evolution of high fecundity must be primarily a response to variability in the environment, and for any highly fecund stock there must exist a minimum level of egg production below which the stock will be unable to reproduce itself."

2. Compensatory mechanisms limiting recruitment. There are a number of compensatory mechanisms which tend to limit the recruits produced by a large year class (Hempel, 1963). Among these compensatory mechanisms are:

a. The rate of cannibalism of adults on larvae is greater with more abundant adults, since other food in the vicinity of the spawning areas would be depleted when the herring are more abundant.

b. Food density is limiting for larger year classes. Thus they grow slower (Anthony, 1971) and are in poorer condition, produce smaller eggs with less yolk; larvae from such eggs survive less well (Hempel and Blaxter, 1963).

c. Larger year classes spawn greater thicknesses of eggs, a greater portion of which are smothered.

d. Larger groups of herring spawn over wider areas which would diminish the compensating effect outlined under c. but which would lead to an additional compensatory effect, namely a greater portion of eggs being deposited in less than ideal places.

e. Competition for food among larvae is greater from a larger spawning, leading to a higher proportion dying of starvation.

3. Interrelationships of density dependent growth, age at maturity, and age at recruitment. Recently there have been apparent changes in age at recruitment to the adult fisheries from a small proportion recruiting at age 3 to a large proportion recruiting at age 3. Concomitant with changes in age of recruitment are increases in proportion of fish maturing at age 3. Size at age 3 also has increased. Thus, age at maturity and recruitment are density dependent. Specifically, age at maturity and age at recruitment decrease with decreasing stock abundance brought about by increased fishing mortality and a series of poor year classes. Earlier recruitment and maturity are partly attributable to compensatory increases in growth (Burd, 1962), due to decrease in intraspecific competition. Environmental factors, specifically temperature, may also be involved.

Biotic environmental factors affecting recruitment

1. Effects of food availability on survival and growth. In the productive waters of Georges Bank and the Gulf of Maine, the levels of primary productivity, prey density, and the composition of prey are not limiting for herring under most conditions. However, there are three relationships among larval herring and their prey that are critical for survival and growth.

First and most important, small zooplankters, *e.g.* juvenile copepods of carapace length less than 0.6 mm (Blaxter, 1965), must be available at the time of yolk absorption in sufficient density to allow initiation of feeding. Variability in the abundance and distribution of these small prey is a major cause of fluctuations in year class abundance.

Secondly, in late winter to early spring the level of productivity is minimal but so are the metabolic rates of larval herring. During some winters, depending on physical factors (temperature and incident light) and the densities of herring larvae and their competitors, prey densities decrease to such low levels that the condition of a major portion of herring larvae may decline irreversibly (Hempel and Blaxter, 1963; Chenoweth, 1970; Sherman and Honey, 1971). Thus prey density in late winter is one of the major factors controlling the size of a herring year class. Density dependent effects on survival (due to competition for food) are minimized by the wide dispersal of the larvae in winter but they limit the potential production of recruits from very large year classes.

Thirdly, I postulate that the zooplankton bloom associated with vernal warming must be closely synchronized with the increased metabolic demands of larvae as water temperatures increase or significant mortality from starvation will occur.

2. Predators on herring. All stages of the life history of herring are extensively preyed upon. Of particular importance are the predators on larvae and juveniles, while predation on egg beds is particularly important when the stock is in very low abundance. Therefore, an understanding of what the major predators are and their abundance relative to that of the herring stock is essential to any realistic model of the recruitment process. At our present state of understanding, a partial inventory of predators on the various life history stages of herring is all that can be provided. Known predators on herring egg beds are moon snails, haddock, cod, and to a limited extent, other fishes. Predators on larvae are the chaetognath, *Sagitta elegans*, planktonic feeding fishes including mackerel, silver hake, and even adult herring, and planktonic feeding birds and marine mammals.

Predators on juveniles and adults are fish including cod, silver hake, and swordfish, marine mammals, and, of course, man. The most significant predator on herring, once they reach the age of two, is man. Population dynamic studies indicate that natural mortality is reasonably stable between year classes from age two onward, but increases with age, while fishing mortality can, of course, vary widely. Thus I believe fishery assessment studies are more important for juveniles and adults than are studies on natural predators. Of course, the extent of predation on herring by other important fishes and marine mammals is important to an understanding of the dynamics of the total ecosystem and to production of the predatory species. For an understanding of herring recruitment, studies of predation on larvae and young-of-the-year are most important.

3. The effect of epidemic diseases on recruitment of larvae. Epidemic diseases are a major cause of fluctuation in the abundance of animals, and herring are no exception. The abundance of the affected stock, the abundance of intermediate hosts, and environmental variables, are significant factors in the incidence of epizootics. Three examples will be provided. Epizootics of a fungus disease of herring (caused by *Ichthyophonus hoferi*) of the western Atlantic have occurred several times. In the Gulf of St. Lawrence four outbreaks have been reported since 1898, while in the Gulf of Maine two outbreaks have been recorded (Sinderman, 1963). Numerous other species of fish are susceptible to infection with *Ichthyophonus*, mackerel being an important one. The possible causes of epizootic outbreaks in herring have been discussed by Sinderman (1963) but the exact cause is unknown.

The second example of high incidence of disease in herring is provided by work done in my laboratory by Sherburne (1973). Erythrocyte degeneration was found in herring along the Maine coast. This disease may be due to infection with piscine erythrocytic necroses (PEN) virus (Walker, 1971). The incidence of this abnormality in herring appears to be closely correlated with temperature. Sherburne and Walker (unpublished) have been able to show that PEN virus occurs with relatively high frequency in several species of fish in the Gulf of Maine area. So far, no direct effect on recruitment or abundance has been demonstrated.

Probably the most important observation relating disease to recruitment in herring is the observation made by Rosenthal (1967) that certain copepod species that are preyed upon by larval herring are intermediate hosts of nematode and cestode parasites of larval herring. It was demonstrated that these parasites could significantly affect the mortality of larval herring.

Although I intuitively conclude that the increased mortalities due to epizootics must have some adverse effect on recruitment, direct measurable effects have not as yet been demonstrated.

Physical environmental factors affecting recruitment and survival

1. Ocean currents. A major physical environmental variable affecting recruitment and survival is the pattern of ocean currents that disperse larvae from the spawning grounds over suitable shoal nursery grounds. This mechanism has been discussed in detail under "Distribution." It will suffice here to reiterate that such mechanisms are essential to larval survival, and fluctuation in their strength or complete breakdown due to prolonged winds or changes in ocean climate is probably a major cause of fluctuations in recruitment. Ocean currents and oceanic fronts, that is, boundaries between water masses, are undoubtedly used by herring stocks as guidelines for migration between overwintering, feeding, and spawning areas. Seriously aberrant conditions could lead to significant losses in later life history stages. Such changes off Iceland and Norway have been shown to lead to changes in availability to "home water" fisheries and even changes and timing in spawning.

2. Temperature. The other major physical environmental variable that seriously affects survival and recruitment is temperature. Temperature requirements and tolerances of Atlantic herring have

already been outlined. Marked delays in cooling of the waters over the spawning grounds have been known to delay spawning in both Georges Bank and Jeffreys Ledge. Such delays could seriously affect survival, particularly from a stock that had already been decimated by overfishing and thus lacked the necessary buffering capacity inherent in a moderately large stock with high fecundity. Mixing of slope water onto the southern edge of Georges Bank with resultant elevating of the temperature above the lethal limit for herring has been known to occur on several occasions during the past decade. In the late 1950's and early 1960's the summer temperatures in the coastal waters of western Maine were elevated to 18° - 20° C. My associate, Stuart Sherburne, and I have observed herring with abnormal hematological patterns directly or indirectly attributable to stress from elevated temperatures (Ridgway, 1971; Sherburne and Ridgway, unpublished observations; Sherburne, 1973). Associations of temperatures and the distribution of herring in the Gulf of St. Lawrence have been demonstrated by Liem, Tibbo, and Day (1957), and an effect of abnormal water temperatures on herring fisheries has been demonstrated by Tibbo and Lauzier (1968). Anthony (1972), page 212, has "obtained a significant regression relating the percent change from spawning stock to recruitment and the temperature at the time of spawning." Lassen (1971) has shown a remarkably direct relationship between the logarithm of the number of recruits (0 group) and the reciprocal of the mean temperature in the latter half of the year for North Sea herring. He used this relationship as the environmental input to his population model.

Towards a model of stock-recruitment - environmental and ecosystem interactions

Introduction

In this section I shall try to move a few steps further in the modeling process by isolating, reiterating, and summarizing certain premises which I believe cover the most critical factors controlling the herring production systems, and by suggesting certain mathematical procedures that can be used for simulation of the system.

Major premises

The major premises that are contained in my conceptualization of the herring stocks being considered are the following:

1. The three stocks being considered can be taken as independent for considerations of stock-recruitment and survival through the first year of life. In formulations involving density-dependent effects on growth and fecundity some competitive interaction among the stocks should be considered.

2. With the exception of density-dependent effects on growth and fecundity, the only variable factor significantly affecting the survival of age groups older than one is fishing mortality. That is to say, natural mortality rates after age one are considered to not depart very significantly from an average value. (The one exception that should be kept in mind is the possibility of catastrophic mortalities from occasional epizootics. However, the likelihood of such epizootics is probably very low at the present low level of finfish biomass.)

3. The major variation in natural mortality occurs during the first year of life. This variation is largely attributable to variations in biotic and physical factors in the environment, but density-dependent mortality also occurs.

4. The major variables in the biotic environment that affect the survival of eggs and larvae are the availability of prey organisms of the proper size when the larvae first begin feeding, the synchronization of the production of food organisms (zooplankton) with the increasing metabolic demands of post-larval herring during vernal warming, and predator density.

5. The major physical environmental variables controlling the survival during the first year of life are temperature and the stability of systems dispersing and retaining larvae on suitable nursery grounds. In the case of temperature, the following variables should be considered: average fall and winter temperature, extreme winter temperature, and delay in the onset of vernal warming. In a search for variables that would describe the stability of the dispersal-retention system on Georges Bank, wind direction, speed, and duration during the fall and winter and measures of losses of shelf water into the slope zone, or intrusions of slope water onto the shelf during October through December should be considered. In addition to direct measurements of the position of the shelf-slope front, and wind measurement, some measure of the stability of the system may be obtainable from the magnitude of freshwater runoff.

Approaches for mathematical modeling

Several modelers of population processes, including Paulik (1973), and Allen and Basasibwaki (1974), have developed simulation stock recruitment models using the age dependent fecundity-survival matrix approach of Leslie (1945). In this approach the fecundity rates of the various ages are arrayed in the top row of the matrix and survival rates of the various age groups are arrayed in the diagonal beginning with the first element in the second row. One of the chief advantages of this approach is that it allows the various age specific effects on survival and fecundity to be isolated. A computer program is available for carrying out the simulation (Gales, 1968) which includes methods for introducing density-dependent effects and for studying competition between species or stocks.

This fecundity-survival matrix takes the following general form (Paulik, 1973):

$$M = \begin{bmatrix} f_0 & f_1 & f_2 & \cdots & f_k \\ s_0 & 0 & 0 & \cdots & 0 \\ \cdot & \cdot & \cdot & & \\ \cdot & \cdot & \cdot & & \\ \cdot & \cdot & \cdot & & \\ 0 & 0 & \cdots & s_{k-1} & 0 \end{bmatrix}$$

f_i = the fecundity rate. This rate is defined as the number of daughters produced per female in the i^{th} age group during the time interval (t, t + 1) who will be alive in the 0^{th} age group at time t + 1.
s_i = the survival rate. This rate is defined as the proportion of females alive in the i^{th} age interval who survive to the $(i + 1)^{th}$ interval at time t + 1.

If $n_{i,t}$ = number of females alive in the i^{th} age group at time t; $i = 0, 1, 2, \cdots, k$
The vector of numbers in each age group at time t is defined as

$$n_t = \begin{bmatrix} n_{0,t} \\ n_{1,t} \\ \cdot \\ \cdot \\ \cdot \\ n_{k,t} \end{bmatrix}$$

We can calculate by matrix multiplication the numbers-at-age vector at time t + 1, $n_{t+1} = Mn_t$.

In the case of the herring stocks under consideration f_0, f_1, f_2 can be taken as zero; estimates of $f_3 \ldots f_k$ can be obtained from the note by Perkins and Anthony (1969). k the oldest age group surviving in significant numbers can be taken as 10.

$$s_i = e^{-Z_i},$$

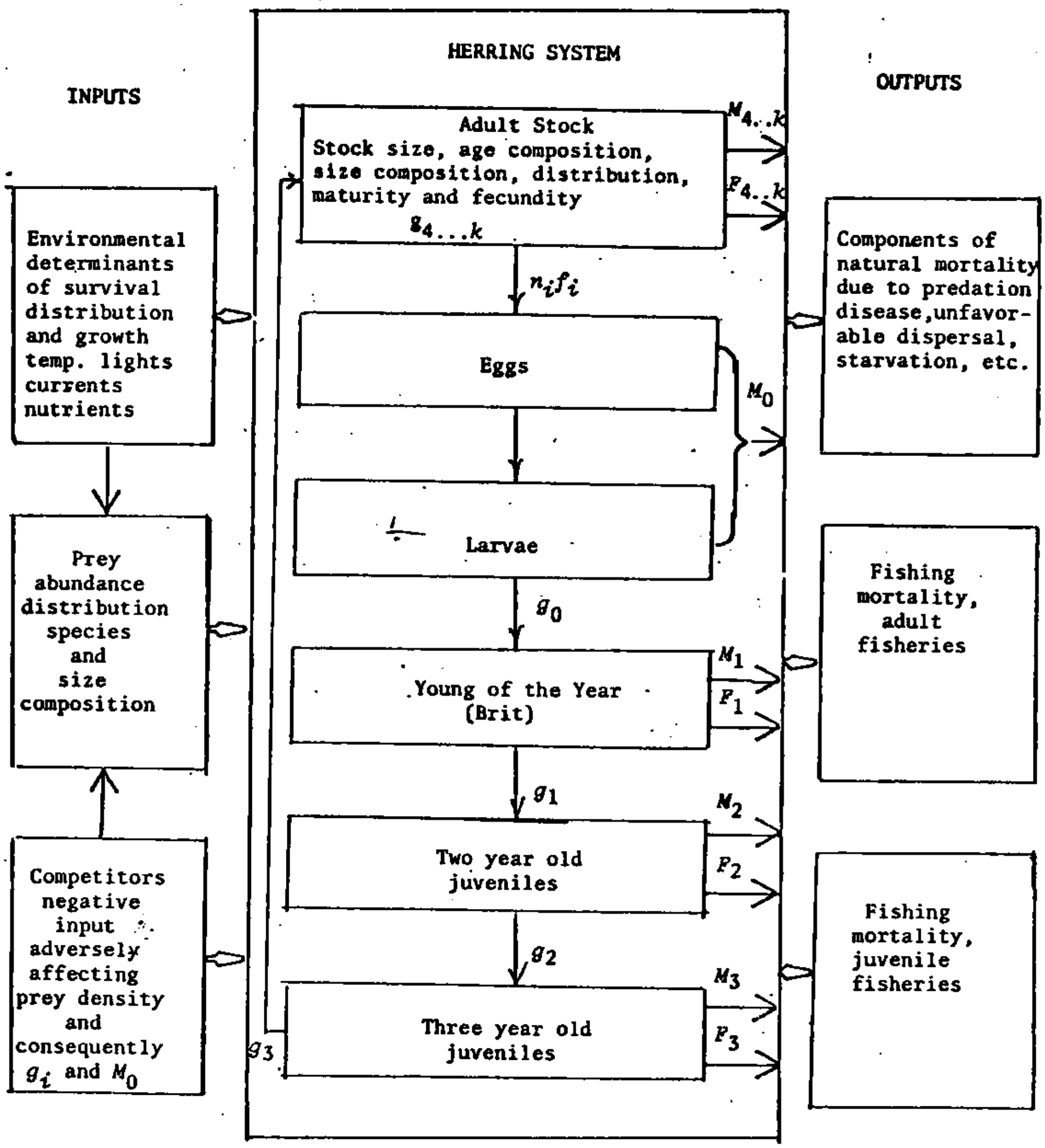
with Z_i the instantaneous total mortality rate for the i^{th} age group in the interval t to t + 1. $Z_i = F_i + M_i$ with F_i and M_i conventionally defined as the instantaneous fishing and natural mortality rates during the interval t to t + 1.

Estimates of stock size and mortality rates are available for the stocks involved (Anthony, 1972; ICNAF Red Book 1973, Part I; ICNAF Summ. Doc. 74/8).

Thus a variety of simulation and analytical treatments can be conducted with this formulation to examine the expected consequences of various management and environmental regimes or scenarios.

For example, following the assumption in this model that the natural mortality rates for age 2 and above are relatively nonvarying, one could vary s_0 stochastically and examine the effects of varying fishing mortality rates. More importantly for the study of recruitment, one can set all values of s_i and f_i except s_0 at an average level (with appropriate adjustments for density dependence) and examine the consequences of varying s_0.

To obtain capability for relating recruitment to environmental variables, s_0 should be related to environmental variables considered to be important, using such multivariate methods as response surface methodology (Box and Hunter, 1962). This method has been used with success in several studies relating multiple environmental variables to recruitment in marine animals and to larval survival, and computer programs for its application are available (Lindsey, Alderdice, and Pienaar, 1970; Lindsey and Sandness, 1970). Of particular interest are the studies of Ramey and Wickett (1973) in which response surface and other multiple regression methods were used to do predictive modeling in which oceanographic parameters were related to recruitment of herring in British Columbian waters.



Notes: g_0, g_1, g_2, M_0, and f_i are density dependent. Portion of 1, 2 and 3 year old fish in juvenile catch varies with year-class strengths. Portion of 3 year old fish spawning and in adult fisheries varies with year-class strength, stock density, and environmental factors.

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