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SPECIAL SESSION ON CHANGES IN FISH POPULATIONS

Changes in the Gulf of St. Lawrnece Herring Populations in the Past Three Decades

by

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ABSTRACT

Atlantic herring Clupea harengus comprise major commercial fisheries in the northwestern Atlantic. In the late 1960s the fisheries developed rapidly after the introduction of mobile fleet operation, and catches increased to a peak of approximately 1 million t - ten times higher than the long-term average. However, in the 1970s almost all herring stocks in NAFO area have declined, and at least two stocks in the Magdalen Islands, Gulf of St. Lawrence, and Georges Bank, Gulf of Maine collapsed.

Atlantic herring populations are characterized by the multiplicity of their spawning grounds. Circumstantial evidence supports the homing hypothesis; i.e. the return of adult fish to the same spawning ground each year. In the Gulf of St. Lawrence there are two separate spawning groups - spring spawners, spawning from late April to mid-June, and autumn spawners, spawning from August to late September. The regularity of spring-spawning time is remarkable, with only a few days earlier in warmer years, and later in colder years. In recent years more summer-spawning herring were seen.

Changes in vital parameters of herring populations in the Gulf of St. Lawrence coincided with the decline in stock size, and a period of environmental changes. There were indications that both density-dependent and density-independent factors played a role in these changes. Recruitment by far was the dominant factor in the spawning biomass production. Several hypotheses were put forward to explain the recruitment variability. Among these are the influence of temperature on spawning success, oceanic forcing on larval retention, predation on young stages, and mackerel/herring interaction. There is convincing evidence that the year-class success is set at an early age, probably before Age 1; but there is no general agreement on the postulated mechanisms.

Circumstances that coincided with the collapse of the Magdalen Islands stock in the late 1970s were compared with those that led to a similar collapse in the Georges Bank stock. It is concluded that the two areas where the stocks collapsed support "critical habitat," transient and fixed habitats in close proximity, that made them vulnerable to fishing pressure by the mobile fleet. The critical habitat hypothesis puts emphasis on the importance of both fishing pressure and environmentally induced variability in herring recruitment.

INTRODUCTION

The southern Gulf of St. Lawrence (NAFO Div. 4T; Fig. 1) supports major fisheries for spring- and autumn-spawning herring. It is the only area in the northwestern Atlantic that still provides spring-spawning herring in large commercial quantities. Except for some small local stocks of minor importance, all other herring stocks are autumn spawning. The herring fishery in the Gulf of St. Lawrence was traditionally carried out with fixed gear (gillnets and traps); and fishing depended largely on the demand for herring as bait, or smoked and pickled for human consumption. Fishing usually occurred from late April to mid June in the spring, and from August to September in the fall.

The fishery rapidly changed after 1965 when large purse-seiners and, to a lesser extent, trawlers started their fishing operation. Drastic changes involved both fishing pattern and magnitude. The fishing fleet increased from a single purse-seiner in 1965 to more than 50 seiners in 1969. Large concentrations of the Gulf herring stock complex were found to overwinter in the fjords along the southwestern coast of Newfoundland (NAFO Div. 3Pn) and east of Cape Breton Island (Div. 4Vn). Large catches attracted the purse-seine fleet to expand their activities - in space and time - to include the whole area in NAFO Div. 4T, 4R, 4Vn, and 3Pn (Fig. 1), and nearly all months of the year. Several reduction plants were constructed, and much of the herring catch was reduced to fish meal and oil until 1970 when demand for food herring increased, particularly after the decline in the Norwegian and North Sea herring stocks.

The lack of significant recruitment, together with the high fishing pressure, resulted in a drastic decline in the herring stocks in the Gulf of St. Lawrence. In 1973, herring catch sharply declined to less than the long-term average since the 1930s. A similar decline in herring stocks in the northwestern Atlantic occurred, but to varying degrees. Two stocks, namely those of the Magdalen Islands (Gulf of St. Lawrence) and Georges Bank, have collapsed in 1979 and 1977 respectively. More than a decade has passed since the collapse, and still the two stocks have not recovered.

The purpose of this paper is to present an overview of the changes in the Gulf of St. Lawrence herring populations in the past three decades, and to provide new information on factors which may have led to the collapse of the Magdalen Islands herring stock.

THE FISHERY

Trends in Catch

Prior to 1965, the herring fishery in the southern Gulf of St. Lawrence (NAFO Div. 4T) was exploited mainly by inshore gillnet fishing on the spawning grounds. Total landings were relatively stable, with a gradual increase from 30,000 t in the early 1930s to approximately 40,000 t in the mid 1950s (Tibbo et al. 1969). An epidemic fungus Ichthyosporidium hoferi resulted in herring mass mortalities, which was reflected in a decline in landings in the late 1950s (Fig. 2). Herring mortalities due to the fungus infection occurred in the spring of 1954, and involved only the spring-spawning stock. Similar mortalities occurred in 1955, but involved both spring- and autumn-spawning stocks. A recovery of herring stocks from this infection occurred in the early 1960s.

In 1965, the fishery dramatically changed after the introduction of the purse-seine fleet, and landings increased sharply to a peak high of approximately 150,000 t in 1970. A similar mobile fleet activity occurred in southwestern Newfoundland, particularly after finding large concentrations of overwintering herring in that area (Winters and Hodder 1975). From a single vessel in the winter of 1964-65, the seiner fleet increased rapidly to more than 50 vessels by 1968-69 (Winters and Hodder 1975). Landings in southwestern Newfoundland reached a peak high of approximately 140,000 t in 1968 and 1969 (Fig. 3). After indications of herring stock decline in both southwestern Newfoundland and southwestern Nova Scotia in 1969, several purse-seiners diverted their effort from these areas to catch herring in the southern Gulf of St. Lawrence. Increased fishing effort is reflected in the high catches in the southern Gulf in 1970 compared to that of southwestern Newfoundland (Fig. 3).

The rapid development of the purse-seine fishery resulted in large quantities of herring catch - much more than market demand. Several large reduction plants were soon constructed to convert herring to fish meal and oil. This trend continued until 1970 when markets for food herring became available in Europe as a result of the decline of herring stocks in the North Sea and the Norwegian Sea. The increased market for Canadian herring resulted in an expansion of fishing operations so that the mobile purse-seine fleet had expanded their activities to include all areas in the Gulf of St. Lawrence and nearly all months of the year (Table 1). Gradually, the herring fishery in the southern Gulf of St. Lawrence changed from a predominantly spring fishery to an increasingly fall fishery, as shown in Figure 4 (Cleary 1982). Similar changes (Fig. 5), inferred from the pattern of gillnet catches from 1949 to 1984, were indicated (Messieh 1987a).

The Magdalen Islands herring stock has been the largest spring-spawning stock in the northwestern Atlantic. Two other spring-spawning stocks in the Gulf of St. Lawrence, namely the Caraquet stock (Area 437) and the Escuminac stock (Area 436), have alternated importance over the years, but they never reached the size of that of the Magdalen Islands. Traditionally, the fishery was based on fixed fishing gear (gillnets and traps) set near the spawning ground. From 1910 to 1966, most of the herring landed at the Magdalen Islands has been caught with traps. Landings compared with herring landings from other Gulf of St. Lawrence herring stocks were reported by Tibbo et al. (1969), and detailed landings and utilization were reported by Spenard (1979). Some 60 to 70 of the 700 commercial fishermen of the Magdalen Islands fished herring for 5 to 7 wk each year with about 20 traps. The fishery was stable and landings fluctuated from 4,000 to 7,000 t (exception: 1918 and 1919) in the period from 1910 to 1949, with an average of about 5,000 t. In the 1950s until the mid 1960s, landings fluctuated between 10,000 and 25,000 t with an average of about 15,000 t. Since 1967, shortly after the purse-seine fleet operation, landings of the traps declined steadily from 25,000 to approximately 1,000 t in 1976, until the fishery collapsed in 1979.

The high rate of exploitation by the mobile fleet resulted in a drastic decline in catch. Landings in NAFO Div. 4T dropped to 20,000 t in 1974. In NAFO Div. 3Pn, landings dropped to 5,000 t in 1973 and almost no catch in 1974. Some of the vessels in NAFO Div. 3Pn ceased operation, and others moved to NAFO Div. 4T and 4Vn. Their increased effort resulted in a modest increase in catch in NAFO Div. 4T, from 30,000 t in 1975 to 40,000 t in 1978, then dropped to 5,000 t in 1981 (Fig. 2). The decline in catch affected all areas in the southern Gulf of St. Lawrence, but the Magdalen Islands stock was hit hardest. Catch quotas introduced in 1975 could not rebuild the stocks, and total landings have been below the total allowable catch (TAC). From 1981 to 1986, catches ranged between 20,000 and 30,000 t against TACs of 15,000 to 32,000 t.

Trends in Catch Per Unit Effort (CPUE)

Effort and catch per unit effort (CPUE) for the purse-seine fleet in the southern Gulf of St. Lawrence is available in detailed form (Messieh 1978). A summary of CPUE (average for 1967 to 1976) shows the distribution and relative abundance of herring in NAFO Div. 3Pn, 4Vn, and 4T (Table 1). The highest averages were shown in the Magdalen Islands (near major spring-spawning ground) and Orphan Bank (a major feeding area). The distribution of fishing effort of the purse-seine fleet reflects the movement of herring to a large extent. In NAFO Div. 3Pn the fishery extended from November to April, catching herring in the overwintering period and at their onset for spring migration from the Newfoundland fjords westward to the spawning and feeding grounds on the Magdalen Shallows.

In NAFO Div. 4Vn, the seiners operated also on overwintering concentrations, and average CPUE in December was 154 t per operative day - the highest CPUE in the whole series. In NAFO Div. 4T, the fishery extended from April to November in the Magdalen Islands and Bay of Chaleur, and from May to November for Orphan Bank and American Bank (Table 1). The April catch represents spring-spawning fish shortly before spawning, and those in November are caught shortly before overwintering. The summer catch represents both feeding concentrations and pre-spawning concentrations of the autumn spawners.

Table 2 presents effort and CPUE for the purse-seine fleet in the Magdalen Islands fishery since its inception in 1967 until its collapse. The statistics shown are of special interest with respect to the fishery collapse, which will be discussed in more detail in a later section of this document. In the first year of the purse-seine operation, fishing was mainly restricted to May (spring-spawning concentrations). In subsequent years, fishing expanded to start in April (pre-spawning concentrations), and in 1968 and 1969 fishing was resumed until November (shortly before overwintering). It is of interest to note that in spite of the decline in herring stocks, the CPUE remained high, until the fishery collapsed - 108 and 109 t per operative day for respectively April and May 1976 (Table 2). The relationship between catch and CPUE for the period 1967 to 1976 (Fig. 6) illustrates this discrepancy.

Messieh (1984) calculated gillnet CPUE from spring and fall fisheries in the southern Gulf of St. Lawrence using the information on all purchase slips available in the Department of Fisheries and Oceans since 1973. CPUE was estimated as catch per successful trip. The lowest fishing trips occurred in 1977 for spring and fall fisheries, with values of 908 and 610 trips respectively (Tables 3 and 4). The highest values were 3,657 trips in 1983 in spring and 3,218 trips in 1985 in autumn. The highest fishing effort was in Escuminac in spring for more than a decade. In autumn, Caraquet and Pictou fisheries were highest, with increased fishing effort in the 1980s. Unlike the purse-seine fishery, the spring gillnet fishery showed similar fluctuations between catch and CPUE throughout the period examined. In the autumn, there was an inverse relationship between catch and CPUE for the period 1973-80, then both increased together until 1985 (Fig. 7).

HERRING POPULATION STRUCTURE

The Gulf of St. Lawrence comprises a complex of herring stocks collectively grouped into two spawning groups: spring- and autumn-spawning groups. In the past, there has been a controversy about the relationship of the two groups. Some authors (e.g. Jean [1956] and Tibbo and Graham [1963]) believed that the two stocks were not discrete and individuals from one group may switch to another, depending on environmental factors. It was not until 1969 when Messieh and Tibbo (1971) conducted an investigation on these stocks, and found evidence for their discreteness.

Later studies were conducted on both sides of the Gulf of St. Lawrence using univariate and multivariate analyses of meristic and morphometric characters, and results confirmed the discreteness of these populations (Parsons 1972; Messieh 1975). More recently, Kornfield et al. (1982), using the likelihood analysis of genetic variations by electrophoretic methods, came to the conclusion that spring- and autumn-spawning groups are genetically different. They also concluded that within a spawning season herring stocks were temporally unstable, indicating no genetic isolation between different components within a spawning group.

Traditionally, the herring fishery in the southern Gulf of St. Lawrence was conducted by fixed gillnets near the spawning ground during spring and autumn. Thus, the majority of fish were in a spawning condition, and they were easy to identify by their maturity stage. However, the stock structure along the Newfoundland side of the Gulf of St. Lawrence appeared to be more complicated than in the southern Gulf of St. Lawrence. In the 1950s, Tibbo (1957) reported that all herring in Newfoundland were spring spawning. However, Olsen (1961) found herring in the late 1950s along the southern and western coasts of Newfoundland displaying spawn over a wide range of months, and the herring were not distinctly spring or autumn spawning.

After the expansion of the purse-seine fishery in the late 1960s, interest has increased in studying the relationship between different herring stocks. The purse-seine fleet was highly mobile and actively catching herring schools inside and outside the Gulf of St. Lawrence. For herring management purposes, it was very important to identify the unit stocks caught by the purse-seiners. An extensive tagging program for herring was initiated in both the Northwest Atlantic Fisheries Center (Department of Fisheries and Oceans, St. John's, Nfld.) and the St. Andrews Biological Station (Department of Fisheries and Oceans, St. Andrews, N.B.). Thousands of herring were tagged in 1970 to 1981 (Table 5). Tagging results were reported by several authors (Hodder and Winters 1970; Winters and Beckett 1978; Messieh 1983).

The tag recoveries from the 1970 and 1971 experiments, in addition to results from meristic and morphometric characteristics, showed that in early spring there was a rapid migration from the overwintering area in southwestern Newfoundland in a westward direction across the Laurentian Channel to the Magdalen Islands (Area 431 - see Table 5 and Fig. 1 for locations). By summer, they have moved on the banks of the Magdalen Shallows (Area 438). Herring concentrations in these areas were composed of spent spring spawners and maturing autumn spawners. By September, spawning had occurred, and in October most herring have aggregated near the "edge" (the western side of the Laurentian Channel) in preparation for the overwintering migration. Based on these results, a composite pattern of herring movement between spawning, feeding, and overwintering areas was produced (Fig. 8).

Results of meristic examination and discriminant function analysis (Messieh 1975) were in good agreement with results of herring tagging (Table 6). Percentage of spring spawners in the Magdalen Islands samples in June, as revealed from the discriminant function analysis, was 86.5%. This agreed well with results of maturity stages. Percentage of mixing of autumn spawners in southwestern Newfoundland ranged from 69.5 to 85.1% (Table 6). This was in contrast to Tibbo's (1957) finding of the dominance of spring spawning in the 1950s. A plausible explanation is that herring populations tend to segregate by spawning group in embayments along the coast. Percent mixing would therefore vary by location and time of sampling. Hodder's (1966) observation that the purse-seine fishery caught mainly spring spawners, while large quantities of autumn spawners were caught in nearby gillnets, supports this conclusion.

There are indications of a change in herring population structure in 1973, coinciding with the heavy exploitation of the early 1970s. In an investigation carried out by Messieh and Longmuir (1978) on herring samples collected in 1973, an overlapping between individual characters, indicating more mixing in the population than in the 1970 and 1971 samples, was observed. Six meristic characters were examined, and the separation between the groups was analyzed by both principal component analysis and cluster analysis (Fig. 9 and 10). The overall results of the two analyses were very similar. In each case there was a tight knit of autumn-spawning groups, all very much alike, and a loosely knit spring-spawning group (Fig. 9). A dendogram based on cluster analysis indicated similar patterns of mixing, particularly within the autumn-spawning group (Fig. 10). Closer amalgamation was shown between the Georges Bank samples (Area 532) and Chedabucto Bay (Area 451), southwestern Nova Scotia (Area 466), and Sydney Bight, Cape Breton Island (Area 470), Magdalen Islands (Area 431) and Sydney Bight (Area 470). These results were received with skepticism because they showed more mixing between herring populations, in disagreement with what had been known about herring movement at that time.

More tagging experiments were carried out from 1976 to 1981 to ascertain the affinity between herring populations in light of this controversy. Results of these tagging experiments (Stobo 1987; Simon and Stobo 1983; Messieh 1983) agreed that there is more mixing between herring populations in and out of the Gulf of St. Lawrence than was originally thought. The tag returns from NAFO Div. 4Vn tagging experiments in 1977 to 1981 showed different results in different years (Table 5). The majority of the tag recoveries from the 1977 experiments came from the NAFO Div. 4Wa winter fishery and NAFO Div. 4Xa summer fishery with a lesser movement into the Gulf. The 1979-80 tagging experiments were conducted farther north in NAFO Div. 4Vn, and the resultant recoveries showed a widespread movement into the Gulf of St. Lawrence. A large number of these returns were from the edge fishery along the Magdalen side of the Laurentian Channel; this fishery has been closed since 1981.

Results of the Souris, P.E.I. (Area 432), tagging experiments showed that both juvenile and adult fish moved to Sydney Bight. Recoveries from fish tagged in Souris, P.E.I., were made within the Gulf of St. Lawrence and a few in NAFO Div. 4Wa; but the majority of recoveries were made in Sydney Bight. These results leave little doubt that the winter fishery in NAFO Div. 4Vn prosecutes a herring stock mixture migrating from 4T, 4WX, as well as local stocks.

It appears that herring have changed their movement pattern compared to earlier years. For example, Parsons and Hodder (1972) conducted a survey on the J.B. Nickerson, March 1971, and compared herring samples collected from

Canso Bank, Banquereau, and the Scotian Shelf with those of the southwestern Newfoundland-southern Gulf of St. Lawrence. Based on differences showed in these samples, they concluded that the southern Gulf of St. Lawrence stocks, which migrate seasonally as far west as the Gaspé and overwinter in the fjords of Newfoundland, do not intermingle to any great extent with herring concentrations along the Scotian Shelf.

A wider dispersion of herring populations during winter appears to have taken place in recent years. This can be seen from winter surveys on the R/V A.T. Cameron and Gadus Atlantica from 1968 to 1976 (Moores and Lilly 1982). The survey catches suggested a much more diffuse pattern of distribution during the overwintering period than was suggested by the results of the tagging experiments in the early 1970s. They have also shown a marked change in the presence of herring in NAFO Div. 3Pn and Div. 4R during the period surveyed (Fig. 11 and 12). In December 1981, Moores and Lilly (1982) discovered concentrations of herring in the area of Great Mecantina Island, North Shore, Québec (NAFO Div. 4S), concurrent with the disappearance of herring from traditional autumn fishing areas in western Newfoundland.

A change in the wintering migration pattern of herring could be interpreted on the basis of a change in age structure of herring populations, as mean age has significantly decreased in recent years. Winters and Hodder (1975) hypothesized that wintering migration of herring from NAFO Div. 4T to Div. 3Pn is age dependent. For both spring and autumn spawners the proportion of the Gulf of St. Lawrence population which migrates to southwestern Newfoundland continuously increases with age from less than 20% for the recruiting age group to 100% for fish older than Age Group 10.

Among the changes which were indicated in the population structure is the apparent increase in summer-spawning fish (Messieh and MacDougall 1984). Summer spawning in the Gulf of St. Lawrence has been indicated in previous years but not to any great extent. Most of the summer-spawned fish were located in the Northumberland Strait and Pictou (Area 433) and Souris, P.E.I. (Area 432).

The complexity of the herring stock structure in the northwestern Atlantic has been discussed by Iles and Sinclair (1982). Several stocks have been described. According to their hypothesis, the number of herring stocks and the geographic location of their respective spawning sites are determined by the number, location, and extent of geographically stable larval retention areas. The associated biological concept is that the gene pool is made up of all of those spawning groups whose larval/post-larval stages come to share the same area of distribution. It follows that it is the physical limits, specifically of the larval and post-larval distributions, that define the biological limits of the stock. Thus, variability in spawning time could be related to environmental variability influencing the larval retention areas.

CHANGES IN VITAL PARAMETERS

Variations in Age and Length

Analysis of age composition of herring in the southern Gulf of St. Lawrence since 1969 showed that the proportion of younger herring in both spring and autumn fisheries has increased in recent years. Mean age in the catch has dropped from 8.4 yr to 3.3 yr in the spring fishery, and from 9.2 yr to 4.7 yr in the autumn fishery (Table 7). Data presented by Winters and Hodder (1975) showed that more than 80% of the catch of the autumn fishery were Age 7 and older during the period 1965 to 1971. During the same period in the spring fishery this percentage was approximately 70%. The change was also noticeable in the number of age groups in the population. In the 1960s and early 1970s there were more age groups (eight groups) than in the 1980s (five groups).

Cleary and Trudeau (1981) reported that the modal length of herring caught in the purse-seine fishery dropped to 25 cm in 1980, and the proportion of fish smaller than 27 cm increased from 7% of the catch in 1973 to 52% in 1980. The modal length in the trap fishery in the Magdalen Islands showed a similar trend (Cleary and Worgan 1981). The catch in 1973, 1974, and 1975 was almost unimodal, with a modal length between 34 and 35 cm. Since 1976 the length-frequency distribution was polymodal, with an increasing proportion of small fish (modal length between 27 and 29 cm) from 1977 until 1980 (Fig. 13). This period coincided with the collapse of the Magdalen Islands herring stock.

The appearance of a strong year class in the fishery could explain the observed drop in the modal length. However, Cleary and Trudeau (1981) excluded this possibility and attributed the length decrease to either overexploitation or to a shift in the area of purse-seine operation. It is evident that the fishing pattern of the purse-seine fleet has changed before the decline in the fishery. It was also clear that the skippers expanded their operation in the mid 1970s to new fishing grounds to compensate for loss of income resulting from a drop in catch. Therefore, it can be concluded that only small fish were available to the fishery.

Data on herring length from samples collected in the southern Gulf of St. Lawrence during the regular groundfish cruises on the R/V E.E. Prince since 1970 are available (D. Clay, Department of Fisheries and Oceans, Gulf Region, Moncton, N.B., pers. comm.). These cruises were carried out regularly during September every year. Length-frequency distributions since 1970 were analyzed (Fig. 14). In the 1970s herring lengths ranged between 16 to 35 cm, with dominant length groups of 26 to 30 cm and 31 to 35 cm. For the first time in 1984 to 1986, the length group of 6 to 10 cm was caught during these surveys (Fig. 14). The source of these small herring was two strata in the Northumberland Strait, the same stations during the last three years of these surveys. These areas were previously identified by Messieh (1979) as nursery grounds for herring.

Variations in Length and Weight at Age

In general, herring weight at age increased from 1969 to 1982 (Table 7), coinciding with the decline in stock biomass. Similar changes were observed for length at age. Cleary and Trudeau (1981) reported that herring of Age 2 to 5 caught during the autumn purse-seine fishery have shown an increase in length at age, mainly during 1975 to 1977. This coincided with the gradual disappearance of smaller fish of a given age. Autumn spawners, up to Age 10, have also shown an increase in length at age. Cleary and Trudeau (1981) indicated that this could result from growth changes and may be attributed to density dependence.

There are contradictions concerning density-dependent growth in herring. Lett and Kohler (1976) found no evidence for density-dependent growth in adult herring in the southern Gulf of St. Lawrence. Winters (1976), on the other hand, concluded that there is density-dependent growth of adult herring but not for juveniles (L_I).

The controversy about density dependence in herring growth is not unique for the southern Gulf of St. Lawrence. Anthony and Fogarty (1985) found density dependence of herring growth in the Gulf of Maine. Growth appeared to be related to both Age 2 abundance and summer water temperature. When abundance is great, its effect overcomes the positive effect of temperature. Moores and Winters (1982) did not find evidence for density-dependent growth in the first year, but suggested density-independent growth in the first year, regulated by temperature. Their conclusions were based on data from herring collected in Fortune Bay, southern Newfoundland (Div. 3Pn). Sinclair et al. (1982) studied herring growth in southwestern Nova Scotia, and concluded that adult growth rate is not density dependent.

Apparently, the difficulty in distinguishing - with certainty - between the density dependence and density independence in herring growth arises from two factors: first, the inadequacy of data used (and this applies to both observed and back-calculated data sets available); and secondly, the complexity of herring stock structure. Messieh (1971) showed polymodality in L_I estimates in the Bay of Fundy herring, reflecting differences in both growth rate and spawning time; and thus, variations in L_I values could arise from varying population mixture. Similarly, Messieh and MacDougall (1984) found summer-spawned fish in the southern Gulf of St. Lawrence, with growth characteristics similar to either late spring-spawned or early autumn-spawned fish.

Variations in Herring Fecundity

Studies on fecundity of herring in the northwestern Atlantic waters are limited. Hodder (1972) reported on fecundity of herring in some parts of the Newfoundland area. Anthony and Waring (1980) and Kelly and Stevenson (1985) reported on herring fecundity in the Georges Bank and Gulf of Maine area. The only studies on herring fecundity in the Gulf of St. Lawrence and Nova Scotia were those by Messieh (1976) and Messieh et al. (1985). The latter includes the longest data series on herring fecundity on both sides of the Atlantic Ocean in recent years.

Comparison of fecundity/length relationships (Fig. 15) showed variations from year to year. Differences were also shown in the relative fecundity (Table 8). Analysis of variance showed that between-year variations are significantly larger than within-year variations (Table 9).

Fecundity data were pooled into two periods: one before 1973 when stock biomass was extremely high, and another period between 1974 and 1983 when stock biomass was extremely low. Comparison of fecundity/length relationships for these two periods showed higher fecundities in the latter (Fig. 16). The coincidence of the increase in fecundity with declining stock size indicates that herring fecundity may be density dependent. Density dependence has been suggested to explain observed fecundity of herring in Georges Bank (Anthony and Waring 1980) and in the Gulf of Maine (Kelly and Stevenson 1985), but there is some disagreement about its general applicability. On the other side of the Atlantic, Nikolski (1969) found that the North Sea herring fecundity was much higher in the 1950s than in the 1930s and attributed this increase to the reduction of their biomass and the increase in food supply. Recently, R. Bailey (Aberdeen Fisheries Laboratory, Aberdeen, Scotland, pers. comm.) observed some variations in fecundity of herring in Scottish waters which may be density dependent.

Results of regression of the logarithmic transformations of weighted mean fecundity on biomass for the spring- and autumn-spawning herring in the southern Gulf of St. Lawrence fitted straight line (Fig. 17a) Correlation coefficients were 0.64 and 0.53 ($P<0.01$) for the two spawning groups respectively. A better fit (correlation coefficients of 0.77 and 0.93) was achieved when regression was run on the dominant size group (300-340 gm) separately (Fig. 17b). These results provide supporting evidence for the density dependence in the Gulf of St. Lawrence herring fecundity. Given the lack of food limitation inferred for adult herring growth at high abundance levels, it is suggested that the increased fecundity at very low population levels may be a compensatory mechanism that is not solely a function of the availability of energy.

Variations in Spawning Time

Prior to 1965 the herring fishery in the Gulf of St. Lawrence was mainly a passive gillnet fishery and catches were predominantly spawning fish. This situation has changed since the introduction of the mobile fleet operation in 1966, and catches were from fish of different maturation during various life stages (Table 10).

Analysis of several thousand maturity stages in the past three decades (Messieh 1987a) showed a remarkable regularity in herring spawning time (Fig. 18). Spring-spawning herring arrive on the spawning ground in late April or early May, and autumn spawners arrive in August and stay until the end of September. Exact spawning time within the spring season varied for only a few days, depending on water temperature. A warmer spring resulted in earlier spawning, and a colder spring resulted in delayed spawning (Messieh 1988).

The fishery around the Magdalen Islands was based solely on spring-spawning herring. In the 1960s spawning occurred from mid April to late May, with peaks from the last week of April to the second week of May. In the 1970s none of the samples provided evidence for significant spawning. The lack of major spawning coincided with the collapse of the fishery and the dominance of non-spawning fish in the limited catches of that period. Partial recovery of the population occurred in the 1980s with the appearance of mature herring on the spawning grounds in 1984 when peak spawning occurred in late May.

In southeastern Prince Edward Island, the spring-spawning period generally extended over a period of 3 wk with considerable variation in the time of peak spawning, which ranged from the second week of May in the 1980s to the first week of June in the 1970s (Fig. 18). Autumn (or late summer) spawning in this area extended over a larger period in the 1980s than in the 1970s, with a major spawning in mid August and early September, in contrast to only early September during the 1960s and 1970s.

In the southern Prince Edward Island and Pictou area (Fig. 18), spring spawning usually occurred during May in the 1960s and 1970s, but there was an extension of the spawning period to late June in the early 1980s, although the peak spawning period in May was approximately the same as in earlier decades. The autumn-spawning period in this area was rather short (4 wk) in the 1960s, became longer in the 1970s (7 wk), and was still longer (11 wk) in the 1980s, with peaks in early August and in early to mid September in the 1970s and 1980s.

In Miramichi Bay, there was very little variation in the timing and duration of spring spawning on the Escuminac grounds (Fig. 18). In some years, the spawning period was limited to only 2 wk. Autumn-spawning occurred off northwestern Prince Edward Island and extended from 3 wk (peak in mid August) in the 1960s to 8 to 9 wk in August and September of the 1970s and 1980s, with peaks in late August and early to mid September.

In the Bay of Chaleur area (Fig. 18), spring spawning extended from late April to early June in all three periods with considerable regularity. Autumn spawning in this area exhibited increased duration of the season, from about 4 wk in the 1960s to 10 wk in the 1980s, with bimodal spawning peaks in early August and early September.

It is concluded that the peak spawning time of herring in the southern Gulf of St. Lawrence generally remained the same during the past three decades. The regularity in spring spawning was more pronounced than during autumn. There is indication that the autumn-spawning period in the 1980s is longer than that in the 1960s and 1970s (Fig. 18). In southern Prince Edward Island and Pictou, the extended autumn-spawning season was more clear than in other areas, and more "late-summer" spawning was observed. This agrees with results from other studies based on otolith morphometrics where summer-spawned fish were described (Messieh et al. 1989). Late summer spawning or early autumn spawning could occur from faster-growing fish in an age group or older fish in the population as hypothesized by Lambert and Messieh (in prep.).

The variations in the timing of spawning for each population within its own seasonally fixed spawning period (a few weeks' duration) agree with the observations of Sinclair and Tremblay (1984), who found that the mean spawning times of different populations differ substantially. They hypothesized that the timing of spawning of a herring population is a function of the time necessary to complete the larval phase and yet metamorphose within the acceptable seasonal envelope. In the southern Gulf of St. Lawrence the seasonal envelope is from April to October.

CHANGES IN BIOMASS AND RECRUITMENT

Adult Stock and Recruitment

Herring stock biomass in the Gulf of St. Lawrence decreased dramatically since 1968. Biomass estimates are somewhat different according to different assessments (e.g. Winters 1978; Cleary 1982; Ahrens and Nielsen 1984), but all of them showed a pronounced decline from 1968, reaching a minimum size in 1978-79, followed by a small increase in 1980 (Fig. 19). The stock decline was shown in both spring and autumn spawners since the development of the purse-seine fishery in 1965.

Winters and Hodder (1975) estimated the decline in spring-spawning stock from 604,000 t in 1965 to 128,000 t in 1971, and then to 82,000 t in 1977. Over the same period, the autumn-spawning stock biomass was reduced from 1,236,000 t to 378,000 t. The adult biomass has contributed 80 to 90% of the exploitable biomass since the mobile fishery began in 1965. Winters and Hodder (1975) concluded that the rapid decline in stock size cannot be attributed solely to the disproportionate removal of biomass. Recruitment to the exploitable biomass has been relatively poor since the mobile fishery developed.

In the spring fishery, the large 1959 year class accounted for over 50% by number of the spring-spawning stock in 1965 and remained the dominant year class until 1970. The 1968 year class partially recruited as 2 yr old, but by 1971 the 1959 year class contributed only about 5% of this stock. In the autumn fishery, the very large 1958 year class comprised nearly 35% by number of the autumn-spawning stock in 1965 and remained dominant until the 1967 year class was partially recruited as 3 yr old in 1970, but by 1971 the 1958 year class was reduced to less than 6% of the stock.

The 1979 year class furnished most of the spring-spawner catch in 1982 and 1983 (77% and 63% respectively). The spring-spawner catches comprised higher percentages of 4 yr olds and younger in 1982 and 1983. The 1977 year class, which dominated autumn-spawner catches in 1981 and 1982, was still quite strong in 1983. However, the 1979 year class provided 40% of the autumn-spawner catch in 1983. More than 50% of the 1982 and 1983 autumn-spawner catches were comprised of fish 5 yr old and older (Ahrens and Nielsen 1984).

Changes in the distribution of herring biomass were investigated since 1971 from data collected during the R/V E.E. Prince research surveys in the Gulf of St. Lawrence in 1971 to 1985 (Fig. 20, 21, 22). In the early 1970s, 65% of the biomass was distributed in the northwestern part of the Gulf of St. Lawrence; the remainder was off southeastern Prince Edward Island and the edge (Fig. 20). In the late 1970s the larger portion (70%) of the biomass shifted to two strata: eastern and southeastern Prince Edward Island (Fig. 21). No fish were found along the edge. In the early 1980s 45% of the biomass was in the northwestern part of the Gulf of St. Lawrence, 30% off northern Prince Edward Island, and 20% off southeastern Prince Edward Island (Fig. 22). Again, no fish were found along the edge.

Factors Affecting Herring Recruitment

Factors affecting herring recruitment in the northwestern Atlantic have been controversial. In the Gulf of St. Lawrence, Messieh (1987b) found no apparent relation between herring stock and recruitment for the period 1976 to 1984 (Fig. 23). In case of spring spawners, a positive correlation was shown when recruitment was plotted against 4+ biomass, but no correlation was found when plotted against 4+5 biomass. In the case of autumn spawners, the correlation was negative for 4+ biomass and no correlation was shown for 4+5 biomass. These results are different from those of Winters (1976) for the period 1958 to 1970 where he described weak relationships between recruitment and biomass ($r=0.52$ for spring spawners, and 0.45 for autumn spawners).

Doubleday (1985) noted that herring recruitment is highly variable at any given stock size, and the correlation coefficients in many cases are not statistically significant. Anthony and Fogarty (1985) noted that the greatest fluctuations in herring recruitment in the Gulf of Maine occurred in the absence of high fishing mortality. Recruitment has varied by a ratio of 20 to 1 since 1947 during a period of underexploitation. Since heavy fishing began in the mid 1960s, recruitment has fluctuated by only a factor of 9 to 1.

Various hypotheses were presented to explain recruitment mechanism of herring in the Gulf of St. Lawrence, but results were not conclusive. An overview of information on this subject was presented by Messieh (1987b) and Grosslein (1987). Both density-dependent and density-independent factors were implied. Density dependence was indicated in fecundity and other vital parameters (see previous section). Winters (1976) noted density dependence in growth of mature herring accompanying the major decline in stock size during the period 1965 to 1973, but Doubleday (1985) argued that density-dependent growth must be weak, as even a doubling of growth rate would result in less than 20% annual growth in weight. The contradictions in the literature concerning the existence of density-dependent growth and maturation in both juvenile and adult herring was discussed by Sinclair et al. (1982).

The effect of total pelagic biomass (herring and mackerel) as a density-dependent mechanism was suggested by Winters (1976) and Lett and Kohler (1976). Results of these two studies were conflicting, and environmental factors, particularly temperature effect on herring and mackerel abundance, were implied. Skud (1982) offered a hypothesis that the response of a species to environmental factors could change from positive to negative, depending on the alternation of dominance between species in the hierarchy in the ecosystem. Skud showed that herring and mackerel alternated as dominant and subordinate species in the northwestern Atlantic since the 1800s. In a recent finding, Messieh (1988) found that mackerel were heavily feeding on herring eggs on the spawning beds in Fisherman's Bank, Gulf of St. Lawrence, and thus could provide a mechanism for this interaction.

An interaction between density-dependent and density-independent factors could add to the complexity of herring recruitment. Winters (1976) noted that large egg production may be inhibitory rather than conducive to the production of strong year classes. He found that egg production levels equivalent to those that produced the large 1958 and 1959 year classes have subsequently resulted in the production of weak cohorts. Messieh and Rosenthal (1989) found in two cases mass mortalities of heavy egg deposition on the spawning beds, which they attributed to sudden change in temperature. The area of the southern Gulf of St. Lawrence where these spawning beds lie is characterized by erratic changes of temperature due to change in wind speed and direction according to Ekman's theory of wind-driven circulation. Figure 24 (Drinkwater, unpubl. data) provides a good example for this phenomenon, which may influence massive and intensive spawn deposition resulting in egg smothering.

Environmental influence on herring recruitment was also implicated by several investigators. For example, Sutcliffe et al. (1977) investigated the effect of environmental factors on catch of several fish species including herring and found significant correlations between these factors and year class strength. Anthony and Fogarty (1985) found that the amount of recruitment per spawning stock was positively related to temperature or other factors (e.g. food availability) related to temperature at intermediate to high levels of spawning stock biomass.

Koslow (1984) noted that large-scale physical processes appear to be responsible for the observed correlation in several fish stocks. Similarities in long-term changes in temperature trends over a wide geographic area of the northwestern Atlantic were shown (e.g. Trites 1979; Welch 1981). Temperature trends in the Bay of Fundy and Gulf of Maine (Fig. 25) during spring showed two warming periods in the mid 1950s and mid 1970s. These periods coincide with similar warm peaks in the surface and intermediate layers in the southern Gulf of St. Lawrence (Messieh 1987).

HERRING STOCK COLLAPSES

The Magdalen Islands Versus Georges Bank

The collapse of the Magdalen Islands herring stock in 1978 occurred only 1 yr after a similar collapse of the largest single herring stock in the northwestern Atlantic in 1977, namely Georges Bank stock. Both fisheries developed rapidly from a small passive fishing gear to a highly mobile fleet operation in 1965-66. A parallel can be drawn from a comparison of the events which coincided with the collapse in two cases; fishing effort abruptly increased, catches jumped to about ten times higher than the average, a peak catch did not last more than a year or two, and there was a steady decline until the stock collapsed (Fig. 26).

A comparison of the fisheries in the Magdalen Islands, Gulf of St. Lawrence, and Georges Bank, Gulf of Maine, provides a unique opportunity for studying the characteristics and dynamics of herring populations and factors influencing their collapse. The two stocks involved were inhabiting contrasting habitats: the Magdalen Islands herring stock is spring spawning, and lies near the northern range of the species' geographic distribution, whereas the Georges Bank stock is autumn spawning, near the southern range of the species' distribution.

The collapse of these two herring stocks provides good examples for highlighting the concept of "critical habitat" in the marine environment.

Anatomy of Change: Magdalen Islands Stock

Coinciding with the period that preceded the fishery collapse was a rapid increase in the mobile fleet fishing operation along the edge, not far from Magdalen Islands inshore fishery (Fig. 27). The mobile fleet rapidly increased from one vessel in 1965 to 50 vessels in 1967. The monthly and annual changes in the fleet distribution patterns showed that the fleet had followed precisely the movement of herring during their three migratory phases: overwintering, spawning, and feeding. Moreover, the trends in effort and CPUE (Table 2; see also Messieh 1978 for detailed pattern of distribution) showed that the fleet had reacted fast in response to the changing situation of the stock and their changing behaviour. Thus, when the overwintering herring concentrations in southern and southwestern Newfoundland (NAFO Div. 4R and 3Pn) declined, the fleet moved fast across the Laurentian Channel to catch fish in eastern Cape Breton Island (NAFO Div. 4Vn) and along the edge. The fleet added some midwater trawlers to reach fish in deeper waters before their ascending movement from the Laurentian Channel to the Magdalen Shallows at the onset of spawning and feeding migration (Fig. 28). The fleet was then joined by vessels from Nova Scotia in 1967 when herring landings in the Bay of Fundy/Scotian Shelf declined.

The decline in herring stock was not detected by the abundance index estimated from the catch rates of the purse-seiners. CPUE stayed at a high level even shortly before the collapse (Fig. 6). This was not the case for inshore trap CPUE, which decreased by a factor of at least 10 from 1967 to 1978 (Spenard 1979). The purse-seine skippers argued that their catches from the edge fishery were from stocks different than those of the Magdalen Islands. Several studies proved that this claim was incorrect (e.g. Parsons 1972; Messieh 1975; Messieh and Longmuir 1978).

The 1959 year class dominated the fishery after 1965 (Fig. 29 and 30) and contributed to the bulk of the catches during 1965 to 1969. Winters and Hodder (1975) estimated the spring-spawning stock in the southern Gulf of St. Lawrence (NAFO Div. 4T) at 604,000 t in 1965 and 128,000 t in 1971 - a reduction of approximately 80%. Recruitment was poor since the late 1960s until the mid 1970s, except for the 1968 year class. This year class was only about one-eighth as good as the abundant 1959 year class, and its effect on the total recruited biomass was insignificant.

The drastic decline in stock biomass was also accompanied by a decrease in the spawning activity in the traditional spawning ground of the Magdalen Islands. There were no spawning surveys in this area, but the spring spawners used to come nearshore in shallow waters and in the semi-closed lagoons of Grande-Entrée and Havre-aux-Maisons; and fishermen would not miss this event. In the mid 1970s the spawn was much reduced and scattered in small patches. Since 1978 no significant spring spawn appears to have taken place (Fig. 31).

Anatomy of Change: Georges Bank Stock

Fisheries for adult herring began on Georges Bank in 1961 by the USSR, and landings amounted to 68,000 t in the first year of operation. Gillnet fishing was the main operation during the first 3 yr, then fishing shifted to otter trawling until 1967. Heavy fishing started in 1967 when Soviet fishermen were joined by other fishermen from 12 countries and the purse-seine fleet was introduced into the fishery. In 1971, a few midwater trawls were added to the purse-seine operation. The catch sharply increased from 68,000 t in 1961 to a peak catch of 374,000 t in 1968 - the largest catch from a single herring stock in the northwestern Atlantic (Fig. 26). Catches steadily declined since then, until 1976 when only 44,000 t were caught. In 1977 the stock collapsed and catches ranging from only 1,000 to 2,000 t were taken from 1977 to 1982, after which a ban on the fishery was imposed. Although the total catch sharply declined, the CPUE effort measured by the mobile fleet statistics stayed the same and even in some cases were higher (see CPUE section; Fig. 6).

Herring recruitment levels to the Georges Bank stock were investigated by Anthony and Fogarty (1985). Two very good year classes (1960 and 1961) supported the fishery with their accumulated biomass until finally they were exhausted (Fig. 30). Year classes of the mid and late 1960s were weak, and the single strong year class of 1970 (Fig. 29) could not support a large fishery.

An assessment of the Georges Bank herring fishery was provided by Anthony and Waring (1980). A summary of their assessment is that with an annual average catch of only 89,000 t from 1961 to 1965 and the presence of three large year classes, the spawning stock increased rapidly from 272,000 t in 1963 to 1.14 million t by 1967. Even without a fishery, the abundance of Georges Bank stock would have declined in the late 1960s due to failing recruitment. The spawning stock size was very large from 1964 to 1969, yet the recruitment was poor (except for the 1966 year class). With fishing, the stock abundance declined very rapidly, reaching 144,000 t in the beginning of 1973. The 1970 year class increased the herring abundance in 1973 by 75% for Age 3 and older, and in spite of a catch of 202,000 t in 1973 the 1974 abundance (Age 4 and older) increased by 138% over the 1973 level. The decline in catch in 1976 and the lack of almost any catch in 1977 make the estimates in 1973 and 1974 very questionable (Anthony and Waring 1980).

Changes in the herring fishery were also reflected in the changes of fishing fleet distribution during 1962 to 1965 reported by Zinkevitch (1967). Information in that report allows the study of behavioural changes of a fishing fleet at the onset of a newly developed fishery, to coincide precisely with the predicted behaviour of herring, and to adjust rapidly to change in this behaviour. This point is discussed in more detail later to show the vulnerability of herring stocks to overexploitation, which can be crucial for the population collapse.

Herring from Georges Bank have been fished by the Soviet fleet since 1961. Herring were distributed over the greatest area during winter. From November to March, herring were fished from 36°N along the continental shelf to the northern extremity of Georges Bank. During that period the herring were active and did not form stable commercial concentrations. In February and March, the bulk of fish was observed in the areas of Long Island, Hudson Canyon, and farther south. In spring, the herring moved from the area of Wilmington and Hudson Canyons to the southern parts of Georges Bank, where they gradually increased in numbers. From May to October, the bulk of fish was feeding or spawning on Georges Bank.

Zinkevitch (1967) reported that herring migration on Georges Bank is related to the development of zooplankton. The greatest biomass of zooplankton was observed in the zone of hydrological front (Fig. 32). Recently, G.C. Harding and K. Drinkwater (Department of Fisheries and Oceans, Scotia-Fundy Region, Dartmouth, N.S., pers. comm.) made similar observations. The formation and redistribution of commercial herring concentrations were indeed related to fluctuations in the borders of the seasonal front, along the northeastern edge of the Bank, which apparently influence the distribution of zooplankton.

Comparison of the distribution of water masses with herring distribution in 1963 to 1965 (Zinkevitch 1967) showed that the major herring fishery coincided with the development of the frontal zone in late summer and autumn (Fig. 27). Changes in the distribution of the Soviet catches between 1963 and 1965, although not discussed by Zinkevitch (1967), showed clearly the precise monthly movement of the fishing fleet in pursuit of the migrating fish. The distribution of the fishing fleet operation has also changed from year to year, reflecting the change in stock abundance. Thus, in 1963 a major part of the fleet effort concentrated on catching fish in their spring migration. In 1964, the fleet expanded its operation throughout the summer and during autumn near the spawning ground. In 1965, a further expansion occurred, and fish were chased after spawning until late autumn in their overwintering migration. Apparently, the development of the herring fishery on Georges Bank was preceded by an intensive Soviet investigation of the distribution of water masses and temperature profiles in the early 1960s to monitor the best hydrographic conditions suitable for herring concentration (Shkinder 1963).

Changes in herring populations on Georges Bank were also shown in the change of time, location, and extent of spawning on the traditional spawning beds. Anthony and Waring (1980) summarized the spawning activities of herring since 1964 (Fig. 31). Spawning bed surveys indicated a significant reduction in spawning area from 1964 to 1971. The spawning was scattered in 1969, 1970, and 1971, producing smaller, diffuse patches of eggs than in previous years. Grimm (1983) noted that although intense fishing pressure was a principal factor in the decline, environmental factors may have played a part. He was referring to large volumes of warm water (>13 C) during the late 1960s and early 1970s which may have affected herring spawning and/or the survival of eggs. It is difficult, however, to believe Grimm's conclusion, because approximately two decades have passed, without any sign of a significant spawning.

Causes of Herring Stock Collapses

Comparing the anatomy of change in the two herring stocks revealed common behavioural and biological characteristics, not different from other herring stocks on both sides of the northern Atlantic. Although the two stocks inhabited contrasting environments, i.e. northern and southern boundaries of herring distribution, their reaction to the fishery was the same.

Common behavioural characteristics include similar schooling behaviour. Schooling appears to be more compact at the onset of spawning. This has been confirmed from the underwater video camera observations on the spawning ground in Fisherman's Bank (Messieh, unpubl. data). This behaviour, evidently, resulted in the rapid decline in the spawning stock biomass without being noticed in the catch rate of purse-seiners. The tendency of the herring population for mixing is another behavioural characteristic. Different mixing rates were shown depending on time of capture (Messieh 1975). Minimum mixing occurred near the spawning bed. More mixing was observed near the edge fishery. Doubleday (1985) noted that wide fluctuations in mixing rates, of the order of 20 to 30%, would lead to corresponding fluctuations of fishing mortality on component stocks of a mixed fishery.

Looking, in retrospect, into the spawning behaviour of the collapsed stocks in the Magdalen Islands and Georges Bank, leads us to the conclusion that a failure in egg deposition, or spawning in small scattered patches, are indications of a declining stock. In the past 2 or 3 yr before the collapse, this was the case in both areas. Causes of the failure to spawn could be a direct interference by the fishing fleet operation on the spawning ground or, as Anthony and Waring (1980) suggested, a "breaking" of the schools by fishing vessels. In the Magdalen Islands, there were reports that spawning has declined because of interference by the purse-seiners and heavy traffic of barges near the spawning beds. The concept of "minimum viable population" was also introduced in an attempt to explain the failure of spawning in other populations (Gilpin 1987), but it could well apply to Atlantic herring.

A common biological characteristic of herring of relevance to the development of commercial fisheries is the existence of only one strong year class in the population at any time. The 1959 year class in the Magdalen Islands and the 1960 year class in Georges Bank were responsible for the accumulation of huge biomass, supporting the fisheries for almost a decade. This characteristic seems applicable to Atlantic herring everywhere. For example, the historical development of the major Atlanto-Scandian and North Sea herring fisheries since the turn of the century involved only a handful of strong year classes (Parrish and Saville 1967). This is also true for other clupeoids such as herring _Clupea harengus pallasi_ in the Pacific coast (Hourston 1980) and the Japanese sardine _Sardinops melanostictus_ (Kondo 1988). Kondo (Tokai Fisheries Research Laboratory, Tokyo, pers. comm.) reported that the stock size of the 1980 year class was 52 times greater than that of 1972. Wide fluctuations in herring recruitment are general features of the clupeoids. The causes of these fluctuations, however, are not well understood nor universally accepted.

Winters and Hodder (1975) noted that the decline in the Gulf of St. Lawrence herring stocks from 1965 to 1971 was due to inadequate recruitment, and that the low recruitment since the late 1950s is probably normal for this stock rather than the exception. Anthony and Fogarty (1985) reported that herring recruitment in the Gulf of Maine since 1947 has varied by a ratio of 20 to 1. Since heavy fishing began in the mid 1960s, recruitment has fluctuated by only a factor of 9 to 1. The greatest fluctuations in recruitment, therefore, historically occurred in the absence of high fishing mortality.

On the other side of the Atlantic, scientists are still not in agreement concerning the causes of the stock decline in the North Sea and Norwegian Sea which took place in the 1960s and 1970s (Parrish and Saville 1967; Saville 1980). Some scientists attributed the decrease in abundance of recruits to environmental changes which have taken place in the North Sea since the late 1940s, and which may have triggered the natural changes in the southern North Sea herring living at the boundary of their distributional areas. The major weakness of the "natural causes" hypothesis is the lack of positive evidence for any of the postulated mechanisms of biological change. Another group believed the effect of the fishery. The "fishing" hypothesis provided an explanation of the causes of the decrease in abundance of the adult Downs stock, but not in the southern North Sea and eastern English Channel. The fishing hypothesis and the natural causes hypothesis lack critical supporting evidence (Parrish and Saville 1967). Two decades have passed since the collapse, and these hypotheses are still debated (e.g. Aberdeen Symposium, Saville 1980).

The Critical Habitat Hypothesis

The weakness of the natural causes hypothesis and the fishing hypothesis reflects the complexity of the biological and behavioural characteristics of Atlantic herring, which were discussed in the previous section. It has been shown that CPUE, particularly of the mobile gear, did not decrease with the decline in herring stocks. Thus, the herring schools maintained their concentration regardless of the stock size. This is an important aspect of species and ecosystem properties, as shown by Boudreau and Dickie (1989) in their biological model of fisheries production.

In the high-enery marine environments, like those near the Magdalen Islands and on Georges Bank, the natural populations exhibit a high capacity for adaptive response to environmental changes. In the two cases the edge areas are subject to varying oceanographic and meteorological forcing which induce variability in availability of fish to fishing gear. Meteorological forcing would influence the development of the seasonal frontal zone in Georges Bank (Drinkwater, unpubl. data) and the location and extent of the cold intermediate layer in the Laurentian Channel near the Magdalen Islands (Messieh 1987c). The environmentally induced variability in availability of fish stands out as a significant problem in many aspects of stock assessment in NAFO areas (Pinhorn and Halliday 1985). This problem, among others, created similar difficulties in herring stock assessments in ICES areas, where the advice consisting of a series of rapidly declining TACs was out of phase with the rate of decline in the stock (Saetersdal 1980).

Dickie (1973) also stressed the point of the influence of both fishing and environmental factors on fish populations. He noted that the capacity for fish populations to respond is significantly affected by changes in population structure and abundance, resulting from selective fishing pressure. That is, fishing dampens the amplitude and thus the natural response to environmental changes.

It would be timely to introduce a new hypothesis: the "critical habitat" hypothesis, that would resolve some of the problems encounterd in the existing hypotheses. This hypothesis may not be new in the fields of freshwater and terrestrial ecology, but - to my knowledge - was not applied to any of the marine fisheries in the northwestern Atlantic.

The two areas, the Magdalen Islands, Gulf of St. Lawrence, and the Georges Bank, Gulf of Maine, where major herring stocks collapsed more than a decade ago and are still in the recovering stage, lend themselves as good examples of critical habitat in the marine environment. Each of these areas supported a major herring fishery which developed rapidly after attracting considerable fishing effort, then completely collapsed before diagnosing the change. The sensitivity of these fishing areas lies in the fact that they support two different habitats, fixed and transient, in close proximity to each other.

Fixed habitat such as the spawning beds of herring have fixed features with tangible physical characters. Of the physical features include tidally induced currents to ensure proper fertilization, oxygenation of eggs, and removal of metabolites. Success of spawning also requires adequate substrate of certain characteristics and depth (spring spawners require different depth than autumn spawners). Obviously, the spawning beds are subject to damage from natural causes as well as from human intervention. Much information on the spawning characteristics and behaviour of herring have been recently gained from the SCUBA diving and video camera observations on the spawning grounds in the Gulf of St. Lawrence (Messieh 1988; Messieh and Rosenthal 1989).

Transient habitats such as the edge of the Magdalen Shallows and the Georges Bank have no fixed boundaries but retain their location by physical oceanographic processs and, thus, are subject to natural variability related to the seasonal and interannual variations in these processes. These areas are crucial as retention areas of larval herring as suggested by Iles and Sinclair (1982) and Sinclair and Iles (1985). These areas are also extremely important for zooplankton aggregations (Harding and Drinkwater, unpubl. data), and as migration routes from the overwintering areas in deeper waters to the feeding and spawning grounds on the banks (Messieh 1987c). Analysis of herring stomach contents showed that the mobile fleet by far caught more herring in the feeding condition than did the gillnet and trap fisheries (Messieh 1979; Fig. 33). The proximity of the transient and fixed habitats in the same fishery - undoubtedly - resulted in an added stress on herring populations, and accelerated their decline.

If the critical habitat hypothesis is accepted, it would require that special regulatory measures for herring fisheries management be imposed in those areas identified as critical, such as the Magdalen Islands and Georges Bank. Among these measures are time and location closures, monitoring the fishing activities on both transient and fixed habitats, and identifying and monitoring the proportions of the individual stock components in the population mixture. Herring populations in Georges Bank would be particularly vulnerable, in light of the potential exploration and development of oil operation and associated heavy vessel traffic.

CONCLUSIONS

In the past three decades changes in vital parameters of herring populations in the Gulf of St. Lawrence were shown. Recruitment by far was the dominant factor in the spawning biomass production. Recruitment variability is influenced by environmental and biological factors as well as fishing pressure, but the relative magnitude of each factor is uncertain.

The circumstances that led to the collapse of herring stocks in the Magdalen Islands are similar to those in Georges Bank. Both stocks were heavily exploited in an area which supports transient and fixed habitats for herring in close proximity. Herring catch in the fixed habitat was predominantly spawners, whereas transient habitat catch was of mixed populations of which the major component was the stock that collapsed.

Due to the close proximity of the transient and fixed habitats in the Magdalen Islands and Georges Bank, it is hypothesized that these areas are critical habitat for herring populations. Fisheries and other human-related activities on these habitats should be carefully monitored and strict regulatory measures imposed.

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Table 1. Seasonal and area distribution of herring purse-seine fleet activity in the Gulf of St. Lawrence, as shown by average CPUE (t per operative day) in 1967 to 1976.

	Area					
			4T			
Month	3Pn	4Vn	Magdalen Is.	Chaleur Bay	Orphan Bank	American Bank
January	96	-	-	-	-	-
February	84	-	-	-	-	-
March	96	-	-	-	-	-
April	41	70	105	107	-	-
May	27	105	93	36	145	30
June	-	-	28	15	43	44
July	21	-	-	80	92	89
August	5	-	-	59	125	72
September	-	-	18	50	141	81
October	-	-	105	63	59	89
November	68	-	108	55	-	35
December	54	154	-	-	-	-

(Source: From Messieh 1978)

Table 2. Fishing effort and CPUE (t per operative day) for the herring purse-seine fleet near the Magdalen Islands, Gulf of St. Lawrence, 1967 to 1976.

	Year									
Month	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976
January E	-	-	-	-	-	-	-	-	-	-
CPUE	-	-	-	-	-	-	-	-	-	-
February E	-	-	-	-	-	-	-	-	-	-
CPUE	-	-	-	-	-	-	-	-	-	-
March E	-	-	-	-	-	-	-	-	-	-
CPUE	-	-	-	-	-	-	-	-	-	-
April E	-	16	19	28	13	-	-	1	24	68
CPUE	-	108	141	106	74	-	-	104	78	108
May E	10	22	9	9	-	9	-	7	92	36
CPUE	115	86	87	63	-	61	-	39	97	109
June E	<1	-	-	-	-	-	-	-	-	-
CPUE	28	-	-	-	-	-	-	-	-	-
July E	-	-	-	-	-	-	-	-	-	-
CPUE	-	-	-	-	-	-	-	-	-	-
August E	-	-	-	-	-	-	-	-	-	-
CPUE	-	-	-	-	-	-	-	-	-	-
September E	-	2	-	-	-	-	-	-	-	-
CPUE	-	18	-	-	-	-	-	-	-	-
October E	-	8	-	-	-	-	-	-	-	-
CPUE	-	105	-	-	-	-	-	-	-	-
November E	-	14	3	-	-	-	-	-	-	-
CPUE	-	113	85	-	-	-	-	-	-	-
December E	-	-	-	-	-	-	-	-	-	-
CPUE	-	-	-	-	-	-	-	-	-	-

(Source: From Messieh 1978)

Table 3. Fishing effort and catch per unit effort of the inshore spring herring fishery in the southern Gulf, 1973 to 1983.

	Caraquet		Escuminac		Shediac		Pictou		Northern PEI		Total	
Year	CPUE	E	CPUE	E	CPUE	E	CPUE	E	CPUE	E	CPUE	E
1973	3.25	669	2.01	1471	0.85	354	-	-	0.95	184	2.09	2678
1974	2.15	492	1.58	1436	0.45	764	-	-	0.36	427	1.23	3119
1975	0.82	238	1.60	1035	0.71	189	-	-	0.99	345	1.29	1807
1976	1.52	356	1.83	1218	0.24	453	-	-	0.49	183	1.34	2210
1977	3.91	67	2.28	546	0.92	140	-	-	0.54	155	1.89	908
1978	4.33	121	2.67	1204	1.22	321	-	-	0.96	377	2.22	2023
1979	1.90	223	1.68	1657	0.59	415	-	-	1.36	275	1.49	2570
1980	2.56	217	1.17	1174	0.63	796	-	-	0.92	236	1.09	2423
1981	0.75	381	0.87	1089	1.19	418	6.81	12	0.82	578	0.92	2478
1982	1.49	509	2.33	687	1.28	612	9.46	6	1.61	455	1.73	2269
1983	1.51	704	2.60	1308	0.96	910	0.63	74	1.76	661	1.79	3657
1984	1.33	217	2.92	657	0.62	132	-	-	0.44	256	1.90	2404
1985	1.20	505	2.95	815	1.52	614	0.92	2	0.76	390	1.81	2326

(Source: 1973 to 1983 from Messieh 1984)

Table 4. Fishing effort and catch per unit effort of the inshore autumn herring fishery in the southern Gulf, 1973 to 1983.

	Caraquet		Escuminac		Shediac		Pictou		North PEI		Total	
Year	CPUE	E	CPUE	E	CPUE	E	CPUE	E	CPUE	E	CPUE	E
1973	2.78	840	3.21	756	-	-	1.55	464	-	-	2.66	2060
1974	6.20	268	3.71	191	-	-	0.97	340	0.21	113	2.99	912
1975	6.76	277	4.59	223	0.09	1	1.27	330	0.25	88	3.63	919
1976	5.18	241	7.44	73	-	-	1.04	337	0.44	40	3.13	691
1977	4.93	383	3.55	16	-	-	1.23	178	0.22	33	3.56	610
1978	4.18	439	4.30	59	-	-	1.05	189	0.38	29	3.21	716
1979	2.57	442	7.34	57	0.06	1	0.98	754	0.99	71	1.78	1325
1980	1.78	496	5.37	120	-	-	0.85	1292	2.69	119	1.45	2027
1981	2.27	1762	4.95	147	-	-	1.15	873	3.24	231	2.15	3013
1982	4.00	1452	1.25	44	-	-	0.74	1542	5.28	23	2.33	3061
1983	4.76	1284	0.77	63	-	-	1.34	748	3.77	264	3.45	2359
1984	3.52	1853	0.77	201	0.75	80	2.83	779	2.46	262	3.02	3175
1985	5.30	1939	0.25	55	8.59	52	3.02	991	5.65	181	4.59	3218

(Source: 1973 to 1983 from Messieh 1984)

Table 5. Results of herring tagging in the Gulf of St. Lawrence, 1970 to 1981.

			Number of tag recoveries at different locations									
			4T									
Tagging location	Release date	Number released (,000)	431	432	433	435	436	438	3P/4R	4Vn	4Wa	4X
Southwestern Nfld.	March 1970	25	64	-	-	-	-	70	391	-	-	-
Magdalen Islands	May 1970	36	65	-	-	-	-	22	89	-	-	-
Gaspé	August 1970	20	-	-	-	-	-	333	579	-	-	-
Southwestern Nfld.	Jan. 1971	10	4	-	-	-	-	19	425	-	-	-
Magdalen Islands	May 1976	10	10	-	-	-	-	-	-	-	2	-
Gaspé	August 1976	28	18	-	-	-	-	148	-	3	3	-
Cape Breton, N.S.	Nov. 1977	3	2	-	1	-	-	-	-	26	80	14
Cape Breton, N.S.	Nov. 1978	4	13	-	1	-	-	2	1	145	19	8
Cape Breton, N.S.	Dec. 1979	11	25	-	17	3	4	11	2	947	22	9
Cape Breton, N.S.	May 1981	3	1	-	3	-	-	-	-	34	1	-
Souris, P.E.I.	Oct. 1978	8	1	35	-	-	1	-	-	3	-	-
Souris, P.E.I.	Oct. 1981	10	1	-	12	-	-	-	-	9	-	-

(Source: From Messieh MS 1983)

Table 6. Percentage mixing of herring by area and month as inferred from discriminant function analysis and meristic characters of herring samples, 1970 to 1971.

Area	Percentage autumn-spawning population											
	Month											
	Jan.	Feb.	March	April	May	June	July	August	Sept.	Oct.	Nov.	Dec.
Magdalen Islands (Div. 4T)	-	-	-	-	-	13.5	-	-	-	-	47.8	-
Prince Edward Island (Div. 4T)	-	-	-	8.8	-	-	-	-	63.3	-	-	-
Escuminac (Div. 4T)	-	-	-	3.2	21.1	-	-	-	84.7	-	-	-
Caraquet (Div. 4T)	-	-	-	-	11.3	-	-	86.5	-	-	-	-
American Bank (Div. 4T)	-	-	-	-	-	-	69.1	51.7	45.4	21.1	-	-
Southwestern Nfld. (Div. 3Pn)	69.5	73.8	72.3	76.7	-	-	-	-	-	-	85.1	-
Sydney Bight (Div. 4Vn)	-	-	-	-	50.0	-	-	-	-	-	-	-

(Source: From Messieh 1975)

Table 7. Changes in mean age in population and weight at age for herring populations in the southern Gulf of St. Lawrence, 1969 to 1982.

	Div. 4T herring			
	Spring		Autumn	
Year	Mean age in population	Weight at Age 4	Mean age in population	Weight at Age 4
1969	8.4	197	9.2	149
1970	8.5	184	8.7	133
1971	7.2	185	8.3	142
1972	6.1	207	8.3	168
1973	6.2	184	7.9	170
1974	5.9	202	7.4	190
1975	5.7	185	8.1	169
1976	6.1	210	8.3	184
1977	5.0	185	8.5	166
1978	4.2	202	6.4	191
1979	4.0	181	6.1	168
1980	3.9	180	4.8	172
1981	4.1	231	4.4	241
1982	3.3	-	4.7	-

(Source: From Cleary 1982; Cleary and Trudeau 1981; Messieh et al. 1985)

Table 8. Estimates of relative fecundity (F/Wt) of two size groups of herring in the southern Gulf of St. Lawrence, for samples collected in 1970 to 1983.

	Size group					
	300 mm group			330 mm group		
Year	N	$\bar{X}$	SE	N	$\bar{X}$	SE
4T spring herring:						
1970	46	241	10.1	18	251	15.5
1971	60	298	8.1	12	229	14.1
1977	-	-	22.3	35	347	14.0
1978	16	296	10.3	97	306	5.9
1979	11	333	12.1	49	325	7.9
1983	20	302	13.6	-	-	-
4T autumn herring:						
1970	92	301	9.8	87	296	12.8
1971	21	399	28.2	34	432	16.3
1977	75	349	9.4	38	440	16.2
1979	29	337	11.7	52	329	13.3
1983	26	410	17.7	11	417	24.5

(Source: From Messieh et al. 1985)

Table 9. Analysis of variance of relative fecundities of Atlantic herring in three different fishery management units.

Source of variation	df	Fecundity/fish weight				Fecundity/length cubed			
		SS	MS	F	PR F	SS	MS	F	PR F
Gulf of St. Lawrence (spring):									
Among groups	7	635393.9	90770.6	22.86	0.0001	0.00008	0.00001	39.49	0.001
Within groups	546	2168126.6	3970.9			0.00016	0.0000003		
Total:	553	2803520.5				0.00024			
Gulf of St. Lawrence (autumn):									
Among groups	5	1127458.0	225491.6	23.12	0.0001	0.00012	0.000024	26.41	0.0001
Within groups	552	5384110.6	9753.8			0.00050	0.0000009		
Total:	557	6511568.6				0.00062			
Nova Scotia (spring):									
Among groups	3	136326.2	45442.1	3.53	0.015	0.000018	0.000006	5.91	0.0007
Within groups	305	3926748.5	12874.6			0.000306	0.000001		
Total:	308	4063074.7				0.000324			

(Source: From Messieh et al. 1985)

Table 10. Percent frequency distribution of maturity stages of herring caught by fixed and mobile fishing gear in the Magdalen Islands, 1966 to 1976.

			Percentage of fish at maturity stage								
Year	Month	Fishing gear	1	2	3	4	5	6	7	8	Number of fish
1966	May	Fixed	-	1.0	8.4	-	15.2	63.6	11.8	-	500
1967	May	Mobile	-	-	-	-	52.0	48.0	-	-	173
	June	Fixed	-	4.0	-	-	-	96.0	-	-	200
1968	May	Fixed	-	-	-	13.5	45.0	41.5	-	-	200
1970	April	Mobile	-	-	1.0	3.0	91.0	3.0	2.0	-	100
	May	Fixed	-	-	-	11.7	24.7	54.7	9.0	-	300
	October	Mobile	1.5	7.1	11.1	30.8	10.1	-	19.7	19.7	199
1971	April	Mobile	0.5	1.0	3.0	25.6	50.3	-	10.1	9.6	200
1973	May	Mobile	-	0.8	77.1	19.1	0.8	-	-	2.3	131
1976	April	Mobile	-	10.5	63.3	15.8	6.5	2.1	-	1.8	400
	May	Mobile	-	10.7	28.2	6.1	3.7	4.6	5.2	41.4	326
	May	Fixed	-	-	-	-	5.9	87.3	4.6	2.3	698

(Source: From Messieh 1978)

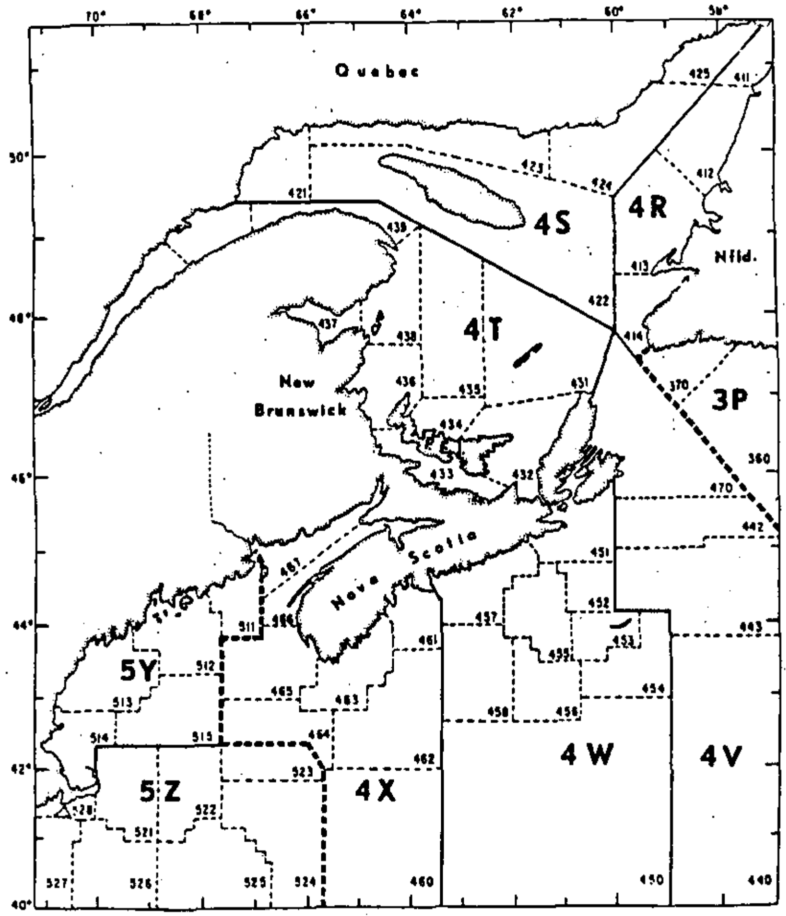

Fig. 1. Map of the northwestern Atlantic, showing NAFO Divisions and sampling areas.

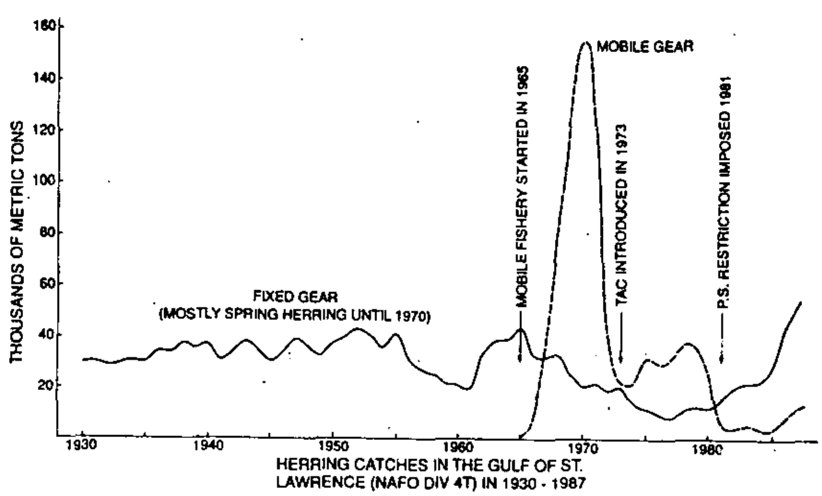

Fig. 2. Herring landings in the southern Gulf of St. Lawrence (NAFO Div. 4T) separated by fishing gear, 1933 to 1987.

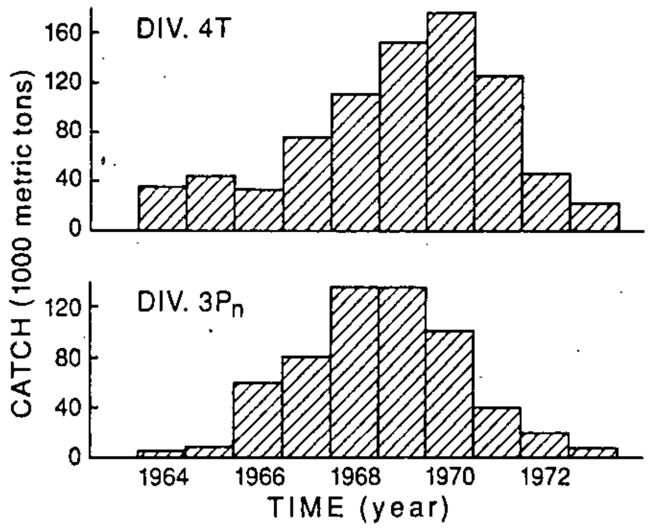

Fig. 3. Comparison of herring landings in the southern Gulf of St. Lawrence (Div. 4T) and southwestern Newfoundland (Div. 3Pn), 1964 to 1973.

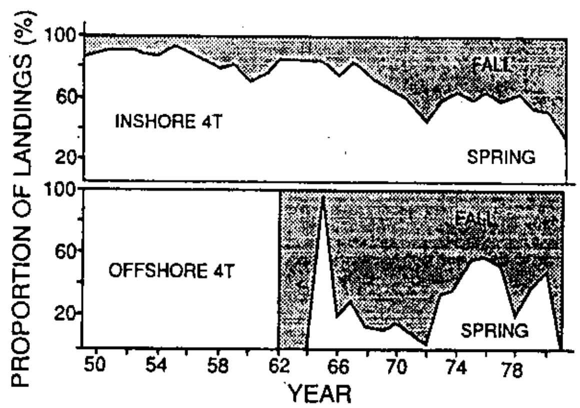

Fig. 4. Changes in the proportion of herring catch in the spring and fall fishing seasons in the southern Gulf of St. Lawrence (from Cleary 1982).

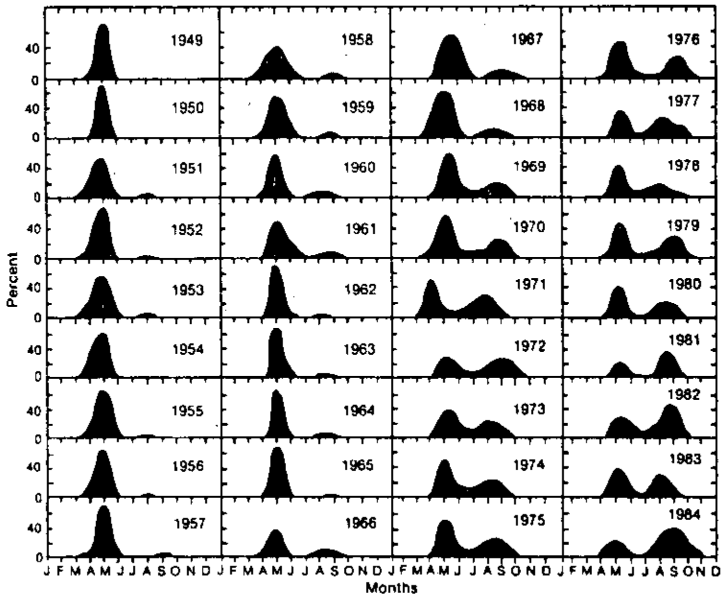

Fig. 5. Relative abundance of spring-spawning herring, as inferred from the pattern of gillnet catches in the southern Gulf of St. Lawrence, 1949 to 1984 (from Messieh 1987).

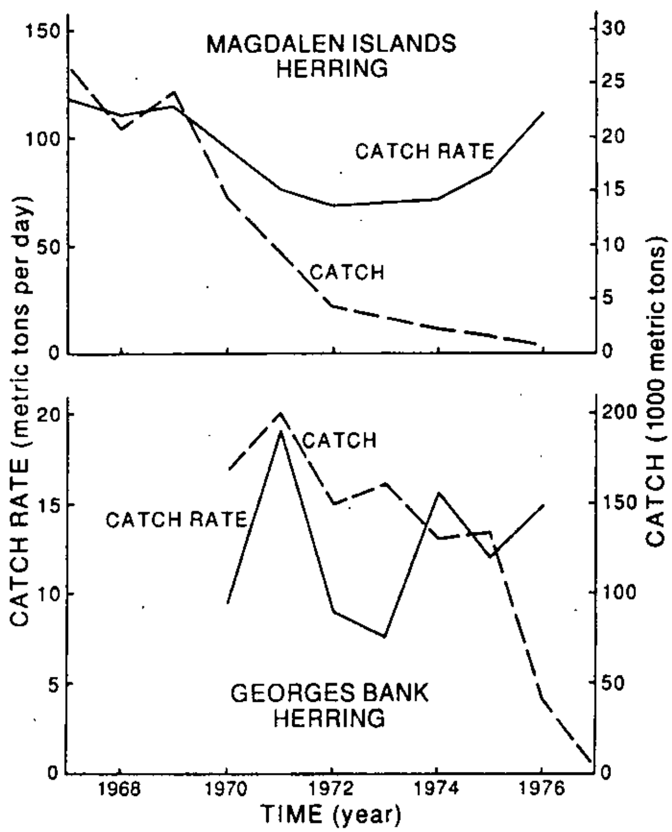

Fig. 6. Catch and CPUE of the herring purse-seine fleet in the Magdalen Islands (upper panel - from Messieh 1978) and Georges Bank (lower panel - from Anthony and Waring 1980).

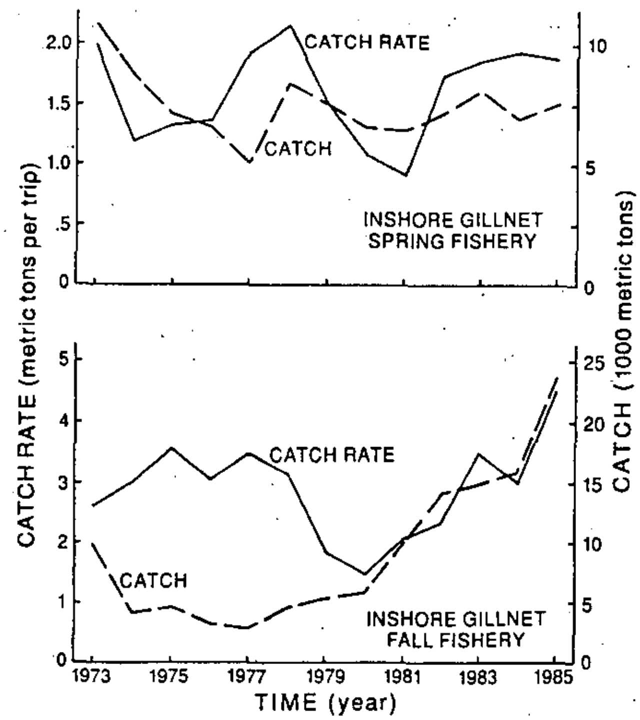

Fig. 7. Comparison of herring catch and CPUE of the gillnet fishery in the southern Gulf of St. Lawrence (from Messieh 1984).

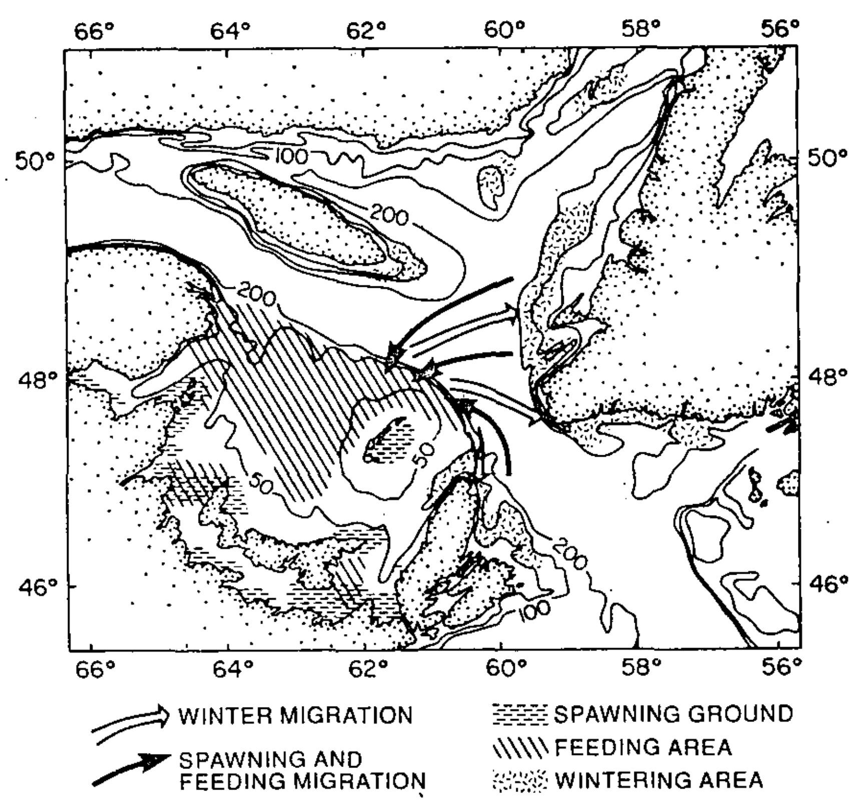

Fig. 8. Pattern of herring movement in the Gulf of St. Lawrence during spawning, feeding, and overwintering.

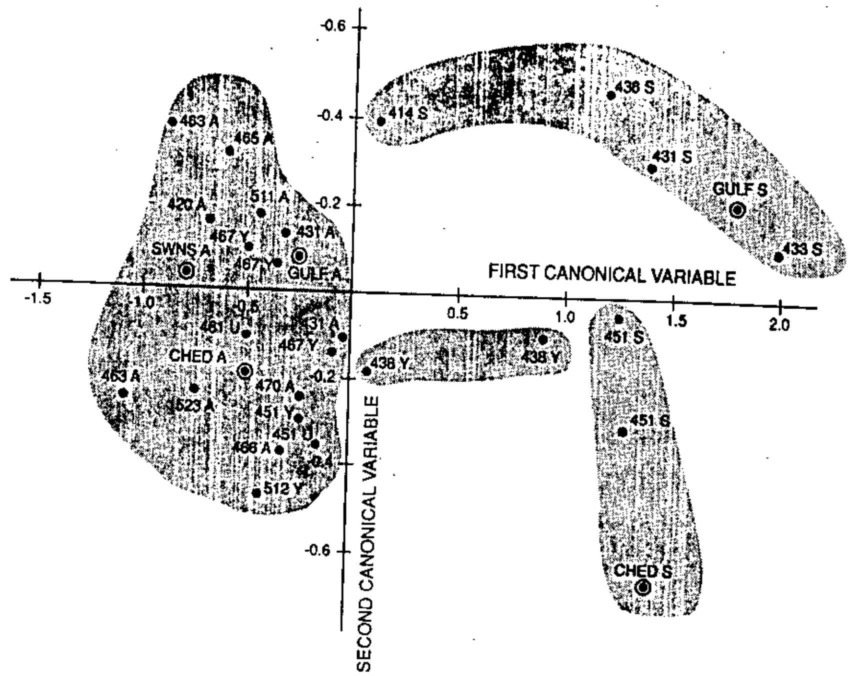

Fig. 9. Canonical variate chart showing the interrelations of herring stocks in the northwestern Atlantic (for sampling areas, see Fig. 1) (from Messieh and Longmuir 1978):

CHED S = Chedabucto Bay, spring
GULF S = Gulf of St. Lawrence, spring
CHED A = Chedabucto Bay, autumn
GULF A = Gulf of St. Lawrence, autumn
SWNS A = southwestern Nova Scotia, autumn

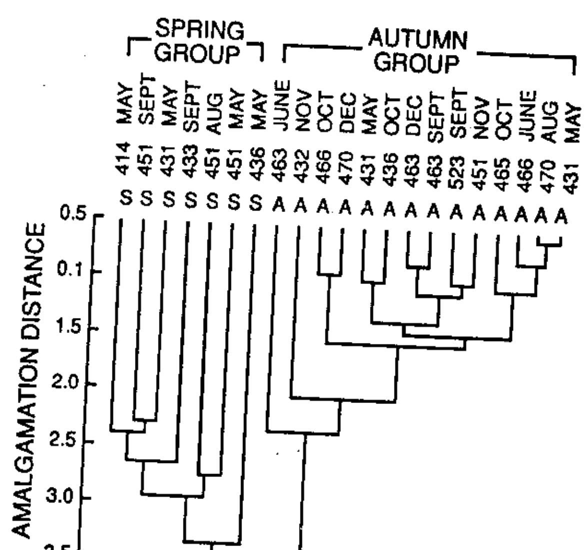

Fig. 10. Dendogram based on the cluster analysis, showing the amalgamation distances between herring stocks in the northwestern Atlantic (for sampling areas, see Fig. 1) (from Messieh and Longmuir 1978).

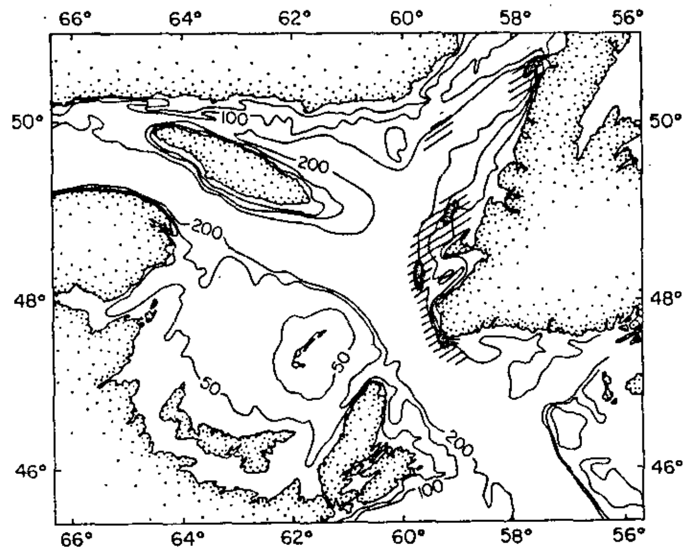

Fig. 11. Winter distribution of herring, 1968 to 1972. Solid area delineates average catch of 10 to 20 kg/tow; etched areas, average catch of 1 to 10 kg/tow (based on data from Moores and Lilly 1982).

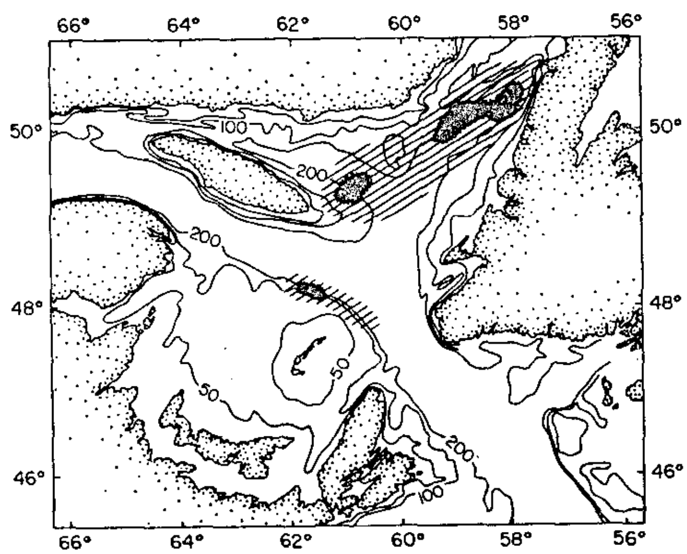

Fig. 12. Winter distribution of herring, 1978 to 1981 (see Fig. 11 for symbols).

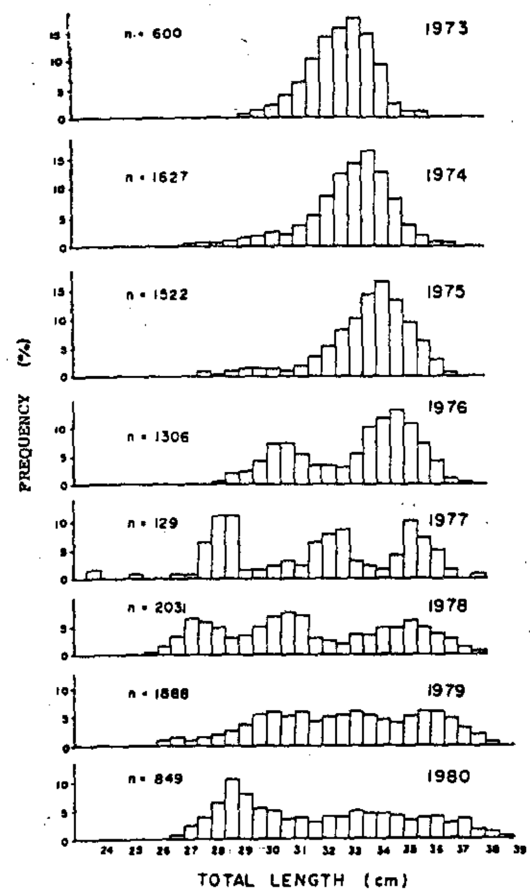

Fig. 13. Length frequency of herring in the Magdalen Islands traps, 1973 to 1980 (from Cleary and Worgan 1981).

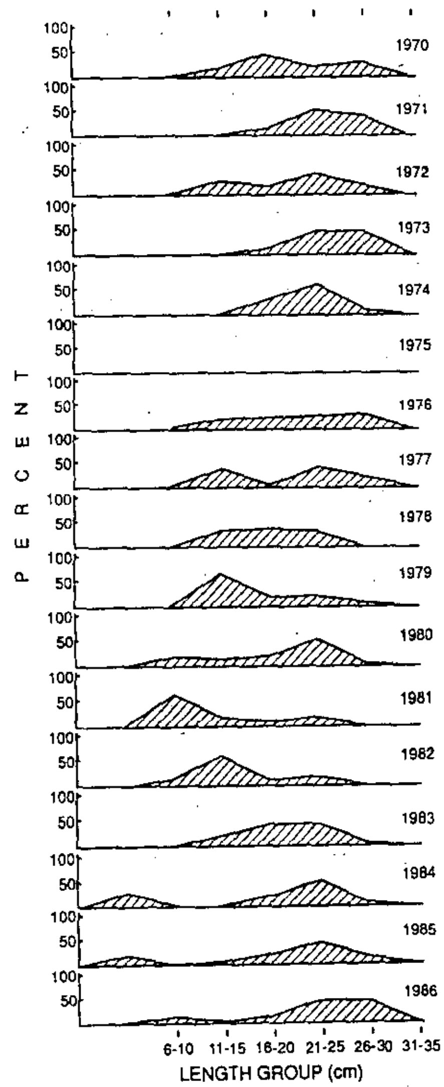

Fig. 14. Length frequency of herring collection from the groundfish research cruise on the R/V E.E. Prince, in the Gulf of St. Lawrence, September, 1970 to 1986.

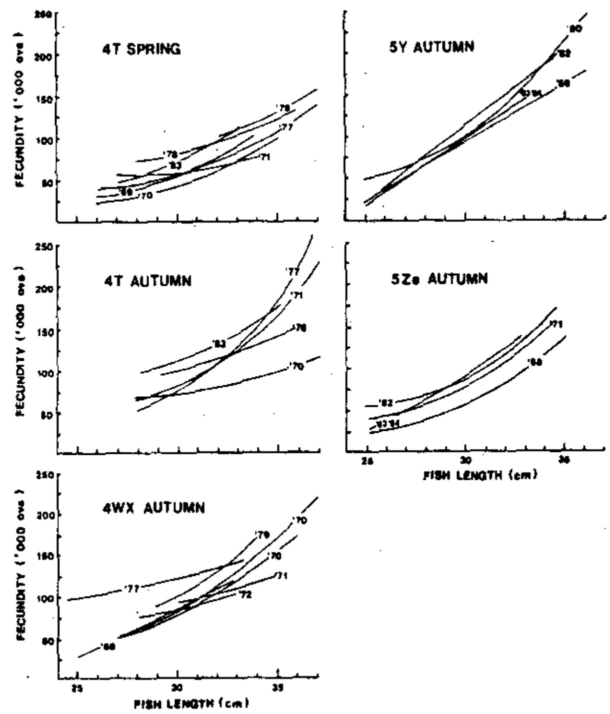

Fig. 15. Fecundity/length relationships of herring from NAFO Div. 4T, 4WX, 4Y, and 5Ze, 1962 to 1983 (from Messieh et al. 1985).

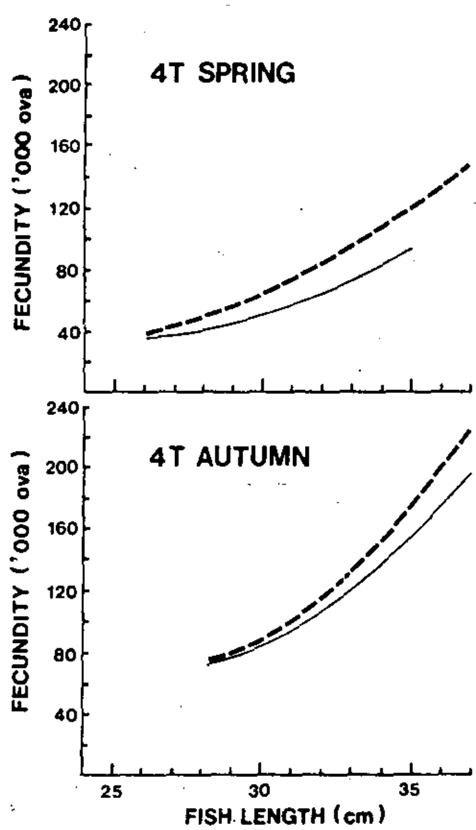

Fig. 16. Fecundity/length relationships of herring sampled before 1973 (——) and after 1973 (-----) in NAFO Div. 4T.

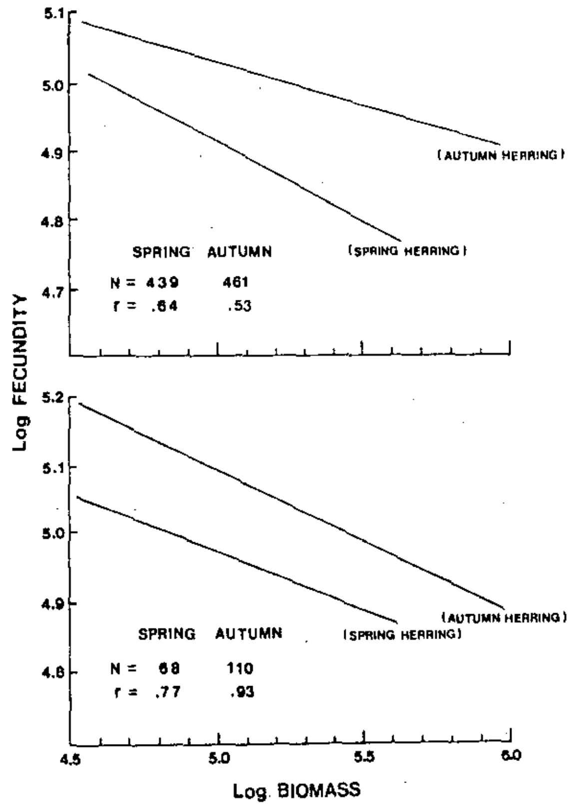

Fig. 17. Regression of herring fecundities on stock biomass: for all sizes combined (upper panel), from one dominant size group, separately.

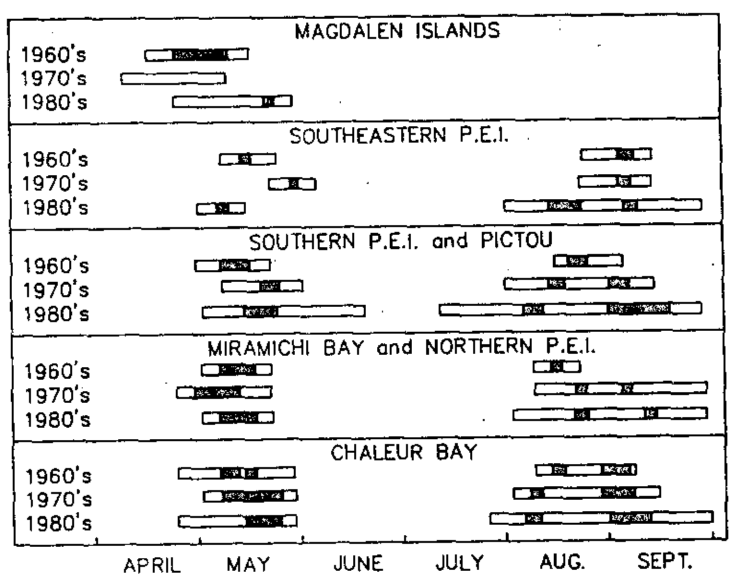

Fig. 18. Time and duration of spring and autumn spawning of herring in the southern Gulf of St. Lawrence in the past three decades, as inferred from analysis of maturity stages. Black bars indicate peak spawning when more than 50% of the fish were mature.

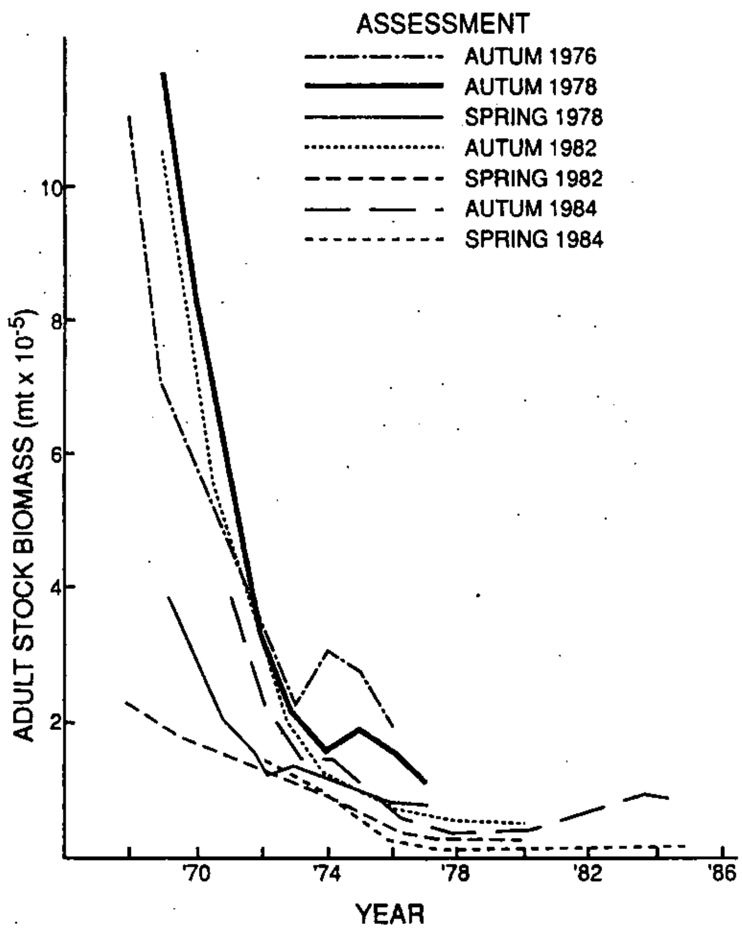

Fig. 19. Adult herring stock biomass estimates in the southern Gulf of St. Lawrence (Age 4 and older - Cleary 1982; Age 5 and older - Winters 1978 and Ahrens and Nielsen 1984), compared to the Georges Bank (Age 4 and older - Anthony and Waring 1980).

Fig. 20:

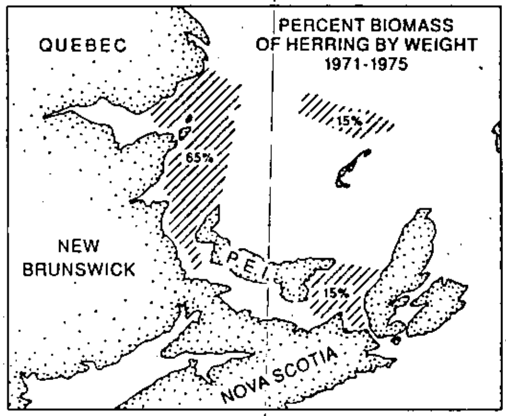

Fig. 21:

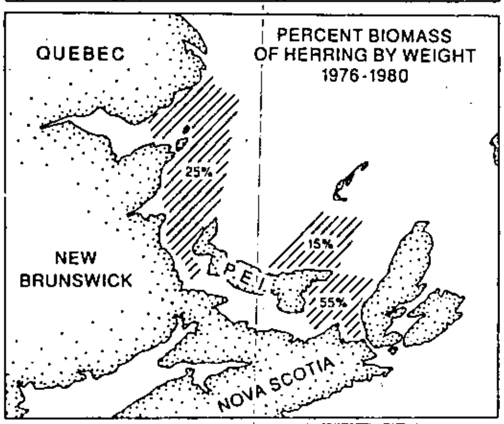

Fig. 22:

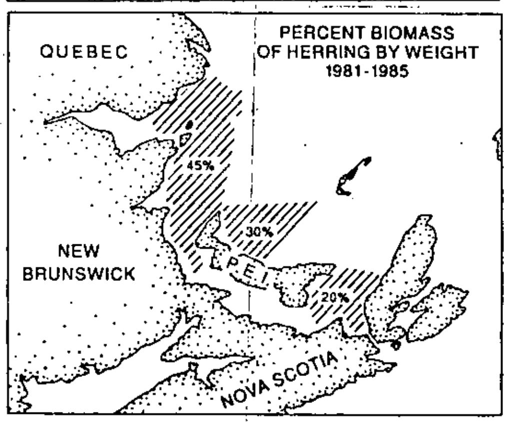

Fig. 20–22. Percent distribution of herring biomass by weight, 1971 to 1985, estimated from the R/V E.E. Prince surveys (based on data from Clay 1984).

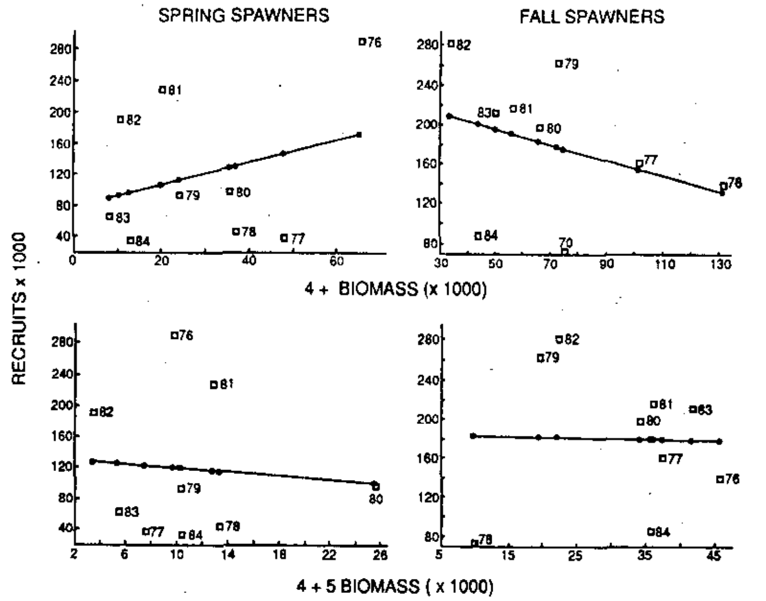

Fig. 23. Relationship between biomass and recruitment of herring in the southern Gulf of St. Lawrence, 1976 to 1984 (from Messieh 1987).

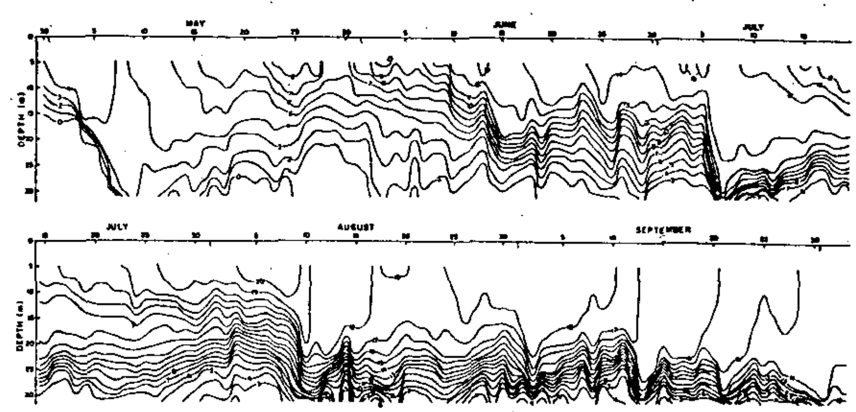

Fig. 24. Time series of isotherm depths in one station in Georges Bay, Gulf of St. Lawrence, near an autumn-spawning bed of herring from April 29 to October 3, 1979 (from Drinkwater, unpubl. data).

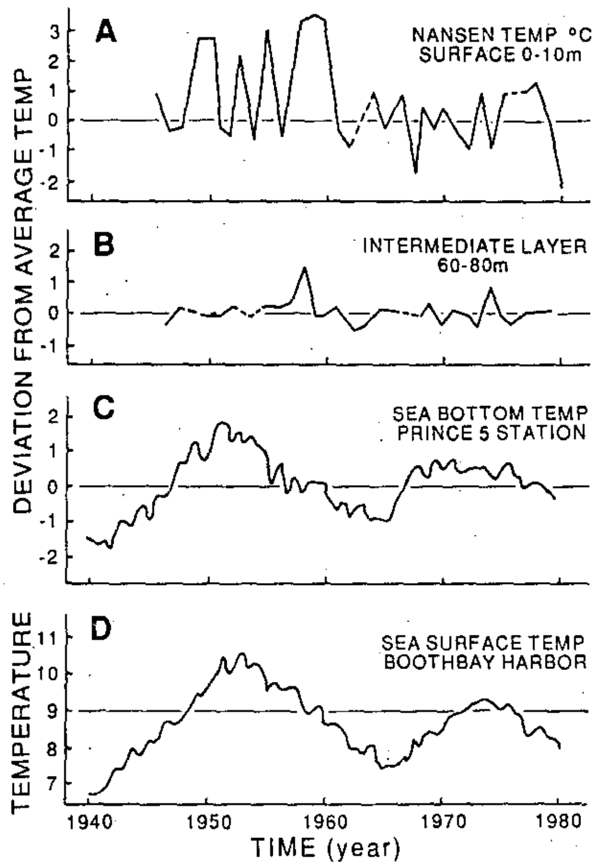

Fig. 25. Trends in sea temperatures during spring, 1945 to 1980:

A - anomalies at surface and intermediate layers (Messieh 1987)
B - anomalies at bottom, Prince 5 Station (Trites 1979)
C - surface temperature at Boothbay Harbor, Maine (Welch 1981).

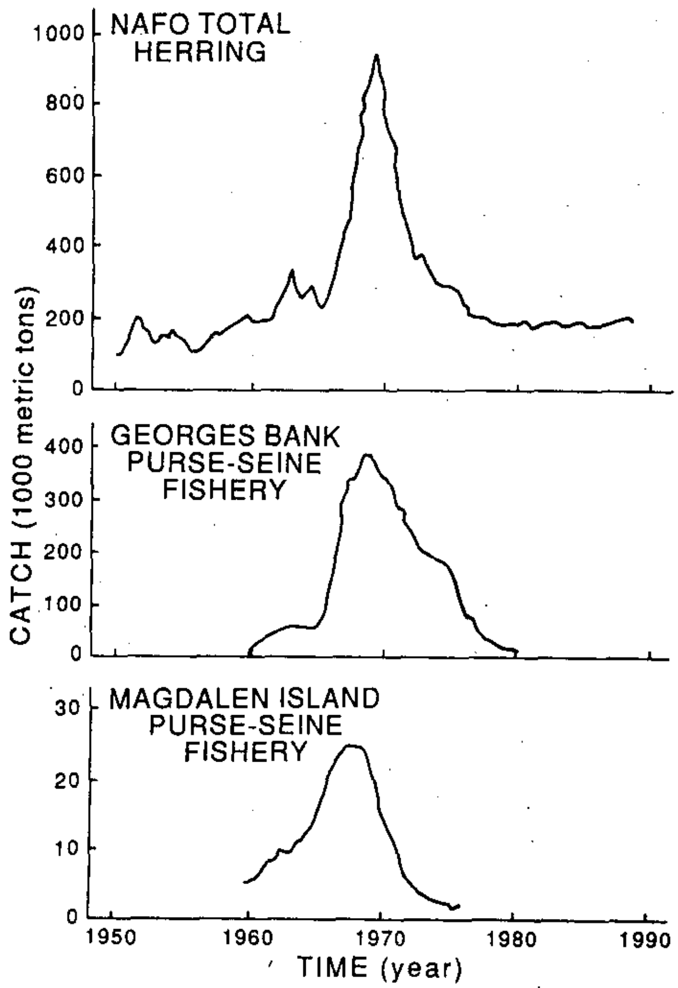

Fig. 26. Herring landings in the northwestern Atlantic (NAFO combined, Georges Bank, and Magdalen Islands).

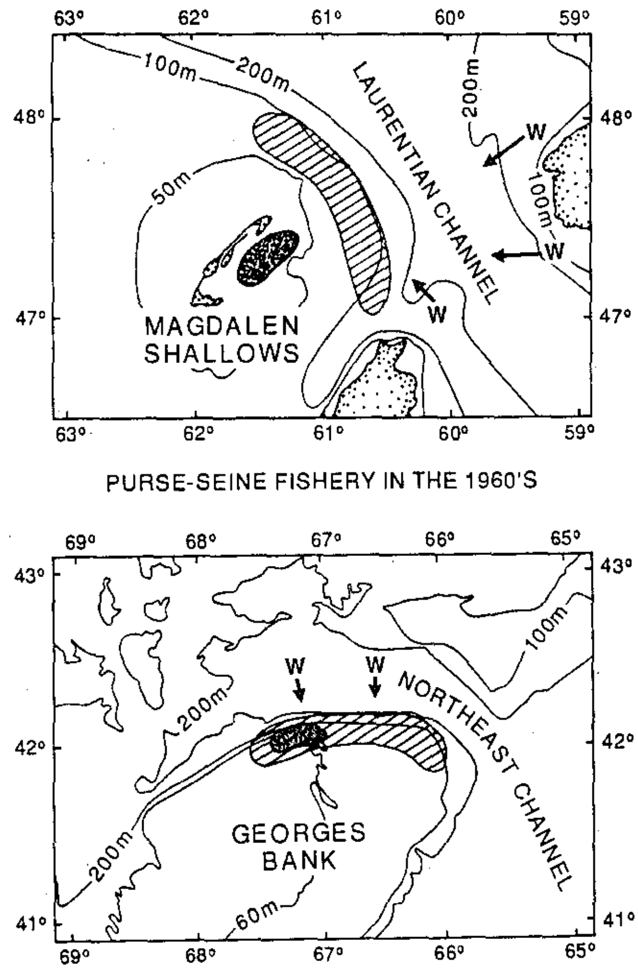

Fig. 27. Distribution of herring catches in the Magdalen Islands and Georges Bank by the mobile fleet in the 1960s, showing concentrations of fish along the 100 m isopleth in both cases (for the Magdalen Islands, Messieh 1978; for the Georges Bank, Zinkevitch 1967 and Halliday et al. 1986).

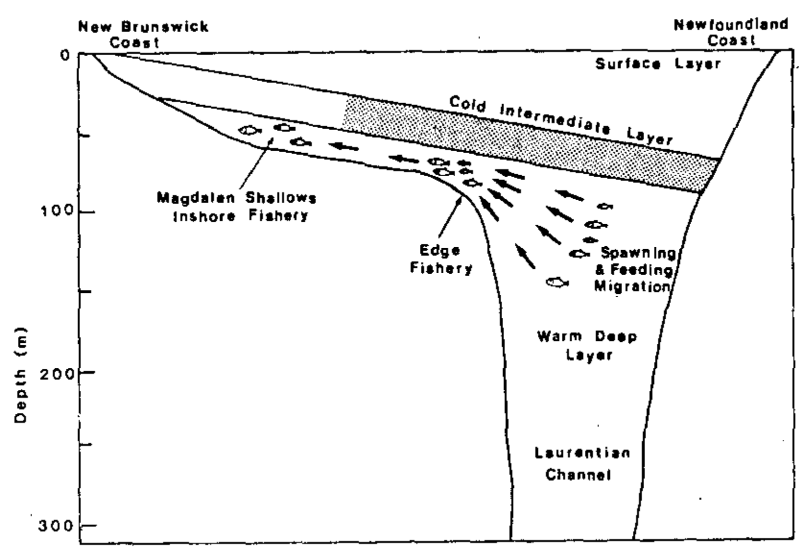

Fig. 28. A model showing herring spring migration from overwintering to spawning and feeding grounds, in relation to the inshore and offshore edge fisheries. It is hypothesized that the depth and extent of the cold intermediate layer would influence the exact timing of herring spawning arrival on the Magdalen Shallows (from Messieh 1987).

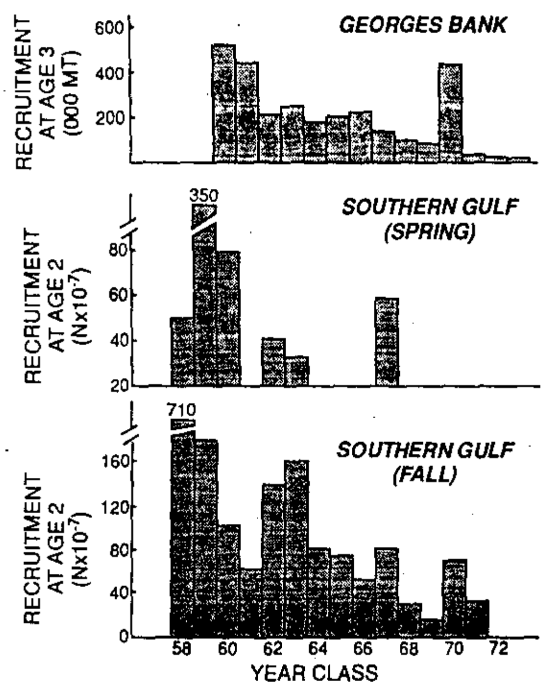

Fig. 29. Comparison of herring recruitment levels to Georges Bank stock (Anthony and Fogarty 1985) and the southern Gulf of St. Lawrence.

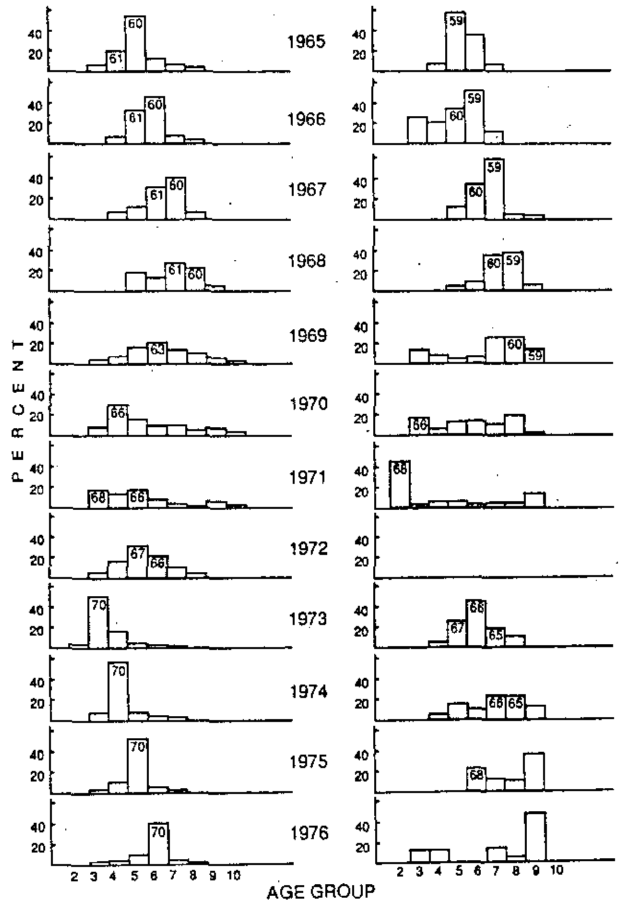

Fig. 30. Age composition of herring catches in Georges Bank, showing the strong year classes of 1960, 1961, and 1970 (from Anthony and Waring 1980); in the Magdalen Islands, showing the strong year classes of 1959 and 1960 (various sources).

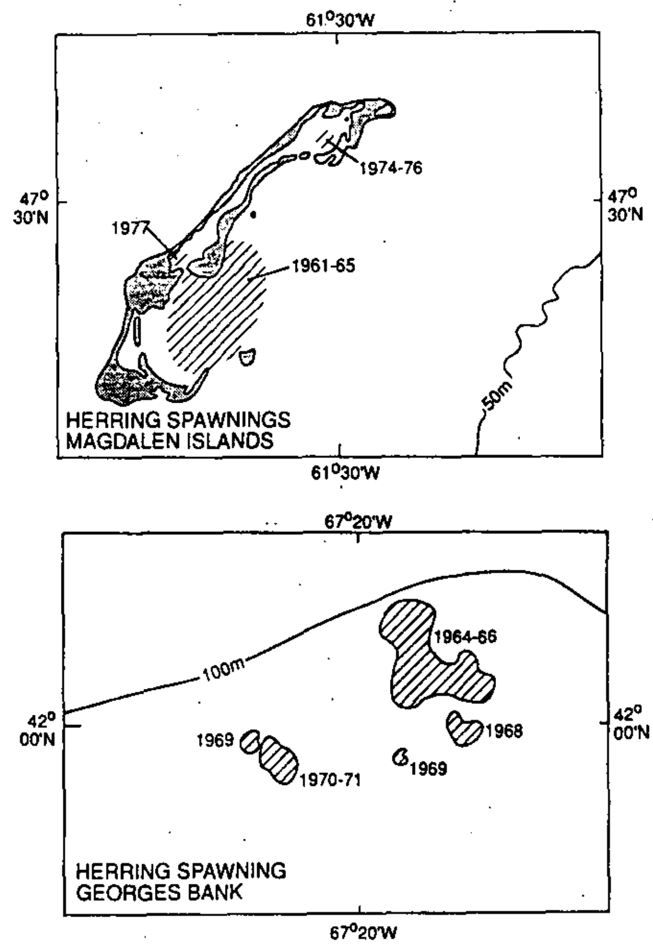

Fig. 31. Changes in the location and intensity of herring spawning beds in the Magdalen Islands (various sources) and Georges Bank (Anthony and Waring 1980).

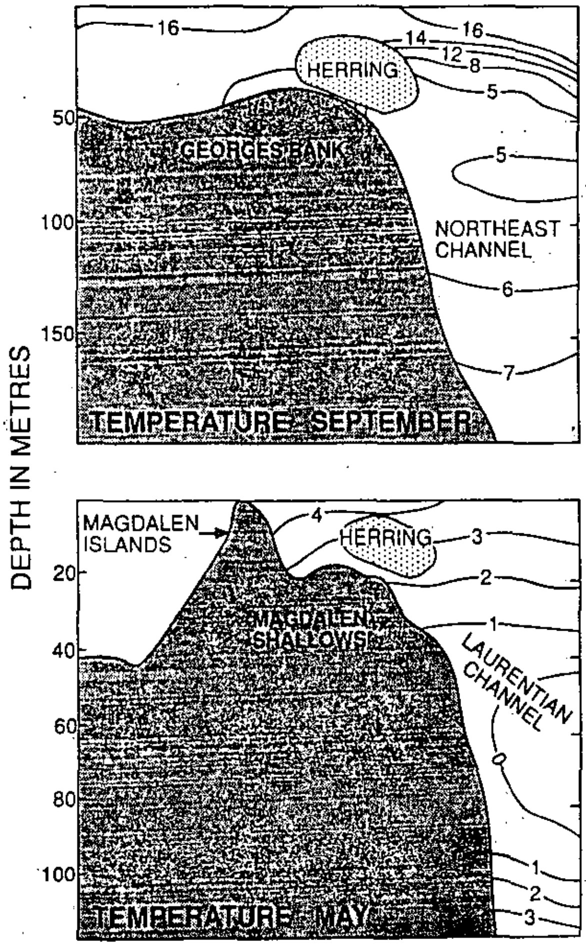

Fig. 32. Vertical sections for temperature distribution near Georges Bank in September (Harding and Drinkwater, unpubl. data), and the Magdalen Islands in May (Messieh 1987). Location of herring schools exploited by the mobile fishing fleet is also shown.

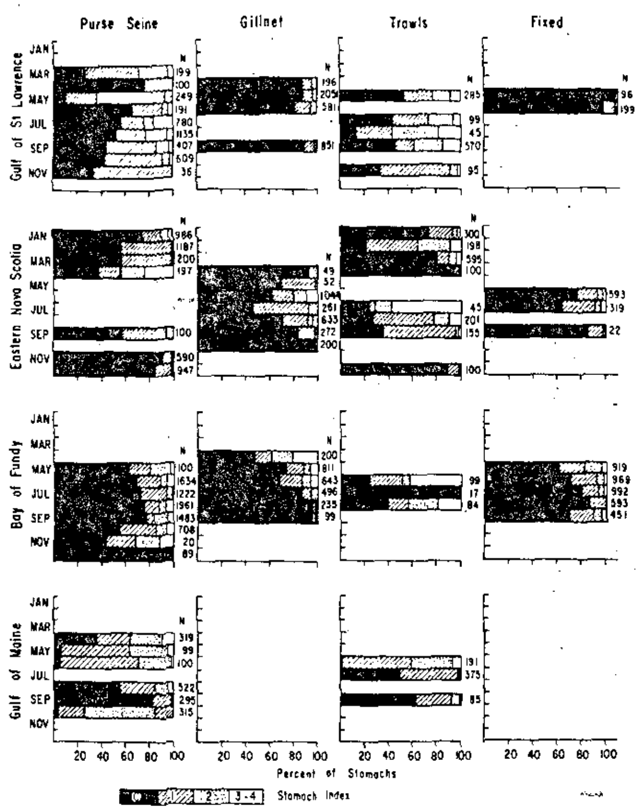

Fig. 33. Feeding condition of herring as shown by the index of stomach fullness (0 = empty; 3-4 = full) caught by different fishing gear in different areas in the northwestern Atlantic (from Messieh et al. 1979).