

Northwest Atlantic



Fisheries Organization

Serial No. N1230

NAFO SCR Doc. 86/103

SCIENTIFIC COUNCIL MEETING - SEPTEMBER 1986

The Enigma of Gulf Herring Recruitment

by

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INTRODUCTION

The southern Gulf of St. Lawrence (NAFO Div. 4T) is a major spawning and feeding area for spring- and fall-spawning herring (*Clupea harengus*). These herring migrate in late fall to overwinter in deep waters along the southwest coast of Newfoundland and east of Cape Breton Island. In April to early May they return to the Magdalen Shallows to spawn and feed. Stock-recruitment relationships for Atlantic herring are poorly understood (Winters 1976). Among the things which are not understood about Atlantic herring in the Gulf of St. Lawrence is when and where recruits join the spawning population. Recruitment occurs mostly during age 3 for spring-spawning herring, and age 4 for fall-spawning. Some herring may not recruit until they are age 4 or 5.

Spawning grounds and spawning times of herring in the southern Gulf are well-known (Messieh 1985). After spawning, the adults leave to feeding grounds. The eggs are left to incubate. Depending on water temperature, spring-spawned larvae hatch after about 3 weeks, and fall-spawned larvae after about 10 days. Little is known of the dispersal of larvae or the distribution of 0-age group. Moreover, it is not known whether juveniles from the Gulf herring migrate outside or stay within the Gulf. It is conceivable that some new recruits may stay within the inshore waters. Occasional juvenile herring surveys (unpublished data) showed 0-group herring in Northumberland Strait, Gaspé Bay, Chaleur Bay and St. Georges Bay. Some recruits seem to migrate offshore, and intermingle with juveniles from other stocks along the east coast of Cape Breton Island (Messieh 1974).

The recruitment mechanism and the stock-recruitment relationships of Gulf herring have been controversial. One of the problems is the inadequacy of data required to test various hypotheses necessary for developing predictive models. According to Sutcliffe (1973) the seasonal changes in the St. Lawrence River runoff plays a dominant role in the productivity and fish abundance in the southern Gulf of St. Lawrence. Winters (1976) examined the effects of this environmental signal on recruitment of southern Gulf herring, and did not find significant relationships between the two variables. Lett and Kohler (1976) and Winters (1976) attempted to explain recruitment mechanisms of the Gulf herring in relation to herring biomass, mackerel biomass, and environmental variations. However, these authors provided two opposing views on the role of density-dependent growth of young herring. Koslow (1984) did not find evidence for the biological interactions among several fish stocks of northwest Atlantic to play a significant role in their population dynamics. He concluded that large-scale physical forcing, rather than biological interactions, predominantly regulates recruitment to northwest Atlantic fisheries. However, Skud (1982), in reference to herring-mackerel interactions, argued that when dominance of a fish species changed, the responses to environmental factors of both the dominant and subordinate species also changed. The changes in dominance between herring and mackerel explained why correlations between temperature and abundance sometimes fail. Skud concluded that a change in response is not acceptable evidence that a climatic factor did not affect abundance or that the observed relation was spurious.

The purpose of this paper is firstly, to review the problems of Gulf herring recruitment, and secondly, to present results of recent studies on herring spawning in an attempt to elucidate the factors which could influence spawning success and subsequent recruitment.

SPECIAL SESSION ON RECRUITMENT

DATA SOURCE AND ANALYSES

The search for herring spawning beds was conducted on Fisherman's Bank (N 46 01 00; W 62 16 00), located southeast of Prince Edward Island, Gulf of St. Lawrence (Figure 1). The Bank covers an area of approximately 6 km². Searches for herring spawn were conducted by 4 SCUBA divers from the end of August until the end of September, 1985. After locating the spawning bed, the boundary was determined by divers using LORAN C. A sampling grid with 200 m intervals between stations was superimposed over the spawning bed. Quadrat samples (each 0.25 m²) were taken using an airlift. In case of heavy egg deposition, samples were not airlifted but cut out from the egg mat within the quadrat. Samples of predators were taken for stomach analysis. Samples of live eggs were collected for bioassay incubation at the Fisheries Research Unit, University of PEI. Egg samples were examined for pathogenic infections at the Fish Health Service Unit Laboratory, DFO, Halifax. Continuous temperature recordings were taken at station near the spawning bed using Ryan's thermograph.

A considerable amount of sea temperature data from 1965 onward were compiled from the Marine Environmental Data Service. All available temperatures from surface to bottom were analyzed along sections crossing the Laurentian Channel at different locations. Meteorological data including temperatures, wind direction and speed were taken from Grindstone Station, Magdalen Island.

Fecundity data were analyzed by year and spawning group. Fecundity/length and fecundity/biomass regressions were fit by the method of least-squares.

RESULTS AND DISCUSSION

Mass Mortality of Herring Spawn in Fall 1985

During the SCUBA survey on herring spawning beds on Fisherman's Bank, southeast PEI, divers observed a spawning bed with heavy egg depositions. Continuous egg carpets of thicknesses between 20 to 30 layers extended over an area of approximately 200 x 500 m. Most of the egg mass on this spawning bed was in a deteriorating condition, showing mass mortality and extended coverage by fungi. From microscopic observations along cross-sections of egg clusters it was obvious that the majority of the eggs (on average 95%) had been fertilized and had reached some stage of development, mostly beyond the blastodisc stage. The near bottom layers had obviously died at an early developing stage (probably late blastodisc, onset of epiboly) while most of the eggs in the 3 top layers contained advanced embryonic stages, which were close to the hatching stage.

Microbiological examination of dead eggs did not show Myxobacteria. None of the isolates obtained are known to be specifically pathogenic for fish or fish eggs. There was no evidence of the presence of *Ichthyoplanus*, the well known fungus disease of herring. Egg batches taken by divers were transferred to the laboratory within a few hours. Live embryos from the top layer continued to develop normally while those located in the second or third layers showed considerable retardation and various malformations. Those located in deeper layers were dying quickly, most of them within 48 hours after transfer. The rate of development seemed to be related to the position within the egg mass. Although most of the eggs (even within the inner region of the cluster) had at least partially gone through epiboly, all eggs below the second layer exhibited embryos with various forms of malformation.

These results showed that the observed mass mortalities of herring eggs were caused by a lack of oxygen, due to the dense packing of the egg layers allowing little separation for water and gas exchange. The relatively thick herring egg capsule requires a higher water velocity in the surrounding medium than other pelagic fish species.

Possible Causes of Egg Mass Mortalities

The question which should be addressed is how such a spontaneous mass spawning had occurred in the spawning bed over such extended area (200x500 m) which resulted in this thickness and packing density, leaving little space between eggs. The fact that the density of egg deposition was unusual can best be demonstrated when compared with observations described from other

areas. From Tibbo et al (1963) calculations on total number of eggs deposited, it can be estimated that the density of eggs was at least two orders of magnitude lower than for most of the bed surveyed during the present study, although most of the eggs were deposited on vegetation. Much lower egg densities were reported by Pottle et al (1980) and Messieh et al (1985) for spring herring in shallow waters in Escuminac, mainly on algae. The number of dead or unfertilized eggs in the spring spawn was negligible. However, high densities of Pacific herring eggs on the spawning grounds in British Columbia, resulting in high egg mortalities had been frequently observed (Rosenthal and Alderdice 1976).

Two possible causes of the spontaneous intensive spawn deposition have been considered. First, it is possible that herring spawning schools could have been disturbed by the fishing boats and drift-nets near the spawning bed, resulting in 'forced' spawning. Forced spawning was reported in earlier surveys in Miramichi Bay (Messieh et al. 1985). However, this possibility was excluded due to the fact that the egg mat was evenly uniform over a wide area indicating natural deposition of eggs. The second possibility could relate the egg mass deposition and consequent mortalities to environmental factors. Previous years showed that herring spawning on Fisherman's Bank usually occurred between mid August and mid September. In 1985, the spawning time was about 2 weeks late. Based on the time of discovering the spawning beds, and taking into consideration the developmental stages of eggs, and an incubation period of approximately 9 to 10 days at temperatures of 15.5°C - 16.5°C, the spawning was estimated to have commenced on September 4 and ended on September 18. Meteorological data indicate that extended cool spring and summer periods prevailed in 1985. This may have prolonged the maturation period of herring resulting in delayed fall spawning.

Sub-surface temperature profiles near the spawning ground showed striking and abrupt changes in temperatures which coincided with the spawning time (Figure 2). No dramatic changes in temperature near the surface were recorded at that time. This indicates that the observed changes in sub-surface temperature were wind-related. According to Ekman's transport, a strong northwesterly wind tends to push the surface waters southward, away from the spawning ground. This would force the sub-surface cold waters to move onto the spawning ground. The reverse occurs during a southeasterly wind. Abrupt changes in temperature could last only a few hours, or up to a day or more. In deeper waters (40 - 60 m) not very far from the spawning site, bottom temperature was 0°C.

It is believed that the sudden changes in bottom temperature have caused the massive and excessive egg deposition, resulting in the observed egg mortalities. Abrupt changes in bottom temperatures on the Magdalen Shallows where the Fisherman's Bank spawning beds occur, are not unusual. Observations were made in 1975 by Drinkwater (pers. comm.) in St. Georges Bay (a few kilometers southeast of the survey area), when a tropical storm passed over. A change in temperature of over 10°C at 30 m in a few hours was observed (Figure 3).

The Effect of Temperature on Herring Spring Migration

The arrival of herring on the spawning and feeding grounds of the Magdalen Shallows (4T area) during spring is a regular annual event. Every year, herring arrive in late April or early May from overwintering deeper waters along the Magdalen Shelf. This regularity in the timing of herring arrival has been known for as many years as any reported observation was documented (Perley 1850). Variations from year-to-year occur; earlier arrival (mid April) in some years, and late arrival (late May) in other years (Messieh, 1977).

Regression of mean day of herring arrival near Magdalen Islands and mean April's surface water temperatures (Figure 4) showed significant negative correlations ($r = -0.86$; $p > .01$). Similar significant correlation was found for 4T area combined, but the correlation coefficient was less than that of the Magdalens ($r = -0.66$; $p > .01$). In order to elucidate the role of temperature in influencing the time of herring arrival on the Magdalen Shallows, variations in temperature from April to November along vertical sections crossing the Magdalen Shelf were analyzed. Several sections were taken, but two sections (G-H; O-P) which are relevant to this study are shown (Figure 5). Section G-H passes from PEI, eastward to Magdalen Islands, Laurentian Channel and southwest Newfoundland. Section O-P passes from North Shore, Quebec, southward to Anticosti Island, St. Lawrence, Gaspé, off Bay of Chaleur until North Point, PEI.

Monthly variations of temperatures from April to November along Section O-P (Figure 6) show the changes in water stratification. In April, the water mass is stratified into two layers: a cold top layer (near 0°C) reaching a depth of about 100 m, and a warm deeper layer (1-5°C) reaching the bottom. In the top layer there was an indication of the beginning of stratification into surface and intermediate layers separated by a weak thermocline. In May, the intermediate cold layer (0°C) decreased in size, forming a cold core along the Laurentian Channel. Meanwhile, stratification of the surface layer continued to proceed, with temperatures ranging from 4.0°C at the surface to 1.0°C at about 50 m depth. In June, the cold core had largely shrunk and in July completely disappeared. Stratification continued to be strong throughout summer, with surface temperatures as high as 16.0°C in August, decreasing to 1.0°C at about 50 m depth. In October, the thermocline in the surface layer began to decay, and in November, the mixing between the surface and intermediate layers was almost complete.

The formation of the cold intermediate layer is a common oceanographic characteristic in the Gulf of St. Lawrence (Figure 7). The onset of spring warm-up and the St. Lawrence run-off are critical in enhancing or delaying the water stratification and subsequently the size of intermediate layer during April and May. A warmer and earlier spring would result in a faster shrinkage of the cold intermediate layer, and vice versa. The depth of the cold layer along the Magdalen Shelf is also influenced by wind direction and speed according to Ekman's theory, where a net transport of water occurs to the right direction of wind. Therefore, a strong southerly wind lasting for a few days would result in tilting up the cold layer on the west side of the Laurentian Channel i.e. along the Magdalen Shelf, whereas a strong northerly wind would result in pushing down this layer (Figure 8).

Wind data for month of April for the period 1951 to 1984 on Grindstone (Magdalen Islands) Meteorological Station were obtained from Environmental Data Services. The prevailing wind direction during April changed from year to year. Mean wind speed ranged between 26.2 km/h in 1979 to 38.3 km/h in 1958. Days with wind speed exceeding 63 km/h ranged from 1 day in April 1973 to 13 days in April 1958. In the latter year, strong southerly storms prevailed for almost half of the month. Temperature anomalies in the Gulf from 1945 to 1980 (Figure 9) showed high temperatures in 1958 in both surface water (0-10 m) and intermediate layer (60-80 m).

Predation on Herring Eggs

SCUBA diving surveys of herring spawning beds allowed direct observation of predation on herring eggs (Messieh 1985). Demersal fish were collected by hand spear. Counts were made of all demersal fish within visual range of two 200-lines which were secured to the bottom. The quantities of herring eggs in the fish stomachs were estimated by volumetric measurement.

Winter flounder (*Pseudopleuronectes americanus*), various Cottidae, Atlantic cod (*Gadus morhua*), are major predators on herring eggs in both spring and fall. For example, 91% of winter flounder collected during spring-spawning herring survey, the mean number of eggs per stomach ranged from 2,000 to 5,000 on different days during the sampling period. Data on abundance of winter flounder on the spawning bed showed a mean density of 0.29 fish per m². On the basis of diurnal feeding periodicity (Frank and Leggett 1984) and feeding frequency of once per day (MacDonald et al. 1982), the estimated loss of eggs during the incubation period due to winter flounder was about 30%. Examination of stomach samples of other predators are not yet completed but it is estimated that total predation on herring eggs was about 60%.

The spawning bed survey on Fisherman's Bank in September 1985 showed that in addition to the list of predators on spring-spawn, Atlantic mackerel (*Scomber scombrus*), Cunners (*Tautoglabrus adspersus*) were heavily feeding on herring eggs. This was the first time to my knowledge that Atlantic mackerel (a pelagic feeder) are reported to feed on herring eggs (demersal). Number of herring eggs in mackerel stomachs ranged from 100 eggs to 29,000 eggs per stomach with mean count of 6,500 eggs. The feeding on herring eggs by mackerel was not incidental. Divers observed schools of mackerel swiftly moving close to bottom, stirring the eggs loose from bottom. The lack of vegetation on a spawning bed, and the relative evenness of the substratum, made eggs more vulnerable for predation.

Herring Larval Production

The southern Gulf of St. Lawrence (4I area) herring populations comprise several stocks collectively classified into spring-spawners and autumn-spawners. Figure 10 shows the major spawning grounds. Spring-spawning grounds are in shallower waters (1-5 m), whereas autumn-spawning grounds are in deeper waters (15-25 m) and further offshore. The regularity in spawning time is remarkable. With a few days from year-to-year variations, spring-spawning occurs in late April/May, whereas autumn-spawning occurs in mid August/September (Figure 11). Incubation of herring eggs takes about 3 weeks in spring, and about 10 days in autumn.

Spawning bed surveys using SCUBA divers (Messieh et al. 1985) showed that spawning occurs in 'waves'. Three or 4 runs were usually observed, with 2 or 3 days between each run. Shortly after hatching, larvae disperse. Larval research surveys showed patchiness of larvae near the spawning beds. Figure 12 shows distribution of herring larvae in 2 successive research cruises, about 2 weeks apart. Observations of larval distributions (Messieh, unpublished) showed that the distribution of larvae coincide with the existence of semi-permanent gyres in the Gulf. Two areas in the Gulf; one in the northern Northumberland Strait for spring-spawned larvae, and another in the southern end of Northumberland Strait for autumn-spawned larvae were identified. In both areas, cyclonic and anticyclonic gyres usually exist (Figure 13).

Lambert (1984) and Lambert and Ware (1984) studied herring larval cohort succession in St. Georges Bay. They suggested that this reproductive strategy serves to limit intraspecific competition and divides a limited food supply more equitably among the total larval population. They discussed how do these reproductive strategies relate to the two major problems facing fish larvae, i.e. predation and starvation. Under the influence of a varying environment, herring elected to use the tactic of "spreading of risk in time". The spreading of risk or bet hedging strategy will reduce the amplitude of fluctuations in numbers, thereby contributing to stability of population size.

Changes in Herring Fecundities

Analysis of herring fecundity data from 1963-1983 indicated density-dependent change (Messieh et al. 1985). More fecundity data were collected in 4I area in 1984 and 1985, and results were in agreement with previous conclusions. Variations in fecundity from year-to-year were shown, with a substantial increase in fecundity in more recent years. Figure 14 shows the regressions of fecundity on length for both spring- and autumn-spawning groups before and after 1973. In all cases, predicted fecundities of herring after 1973 were significantly larger than those prior to 1973. Regression of fecundity on biomass (Figure 15) showed significant correlations between the two variables ($r = .64$, $p < .01$ for all fish combined; $r = .77$, $p < .01$ for dominant size group).

A reasonable explanation for the observed increase in fecundities in recent years is the decline in abundance of herring which occurred in all herring fisheries in northwest Atlantic. Kelly and Stevenson (1985) reached to a similar conclusion for Gulf of Maine herring. There are still some disagreements among biologists on the question of density-dependence of fecundity of Atlantic herring, and its role in regulating the population. Nevertheless, it appears that there is a general acceptance that density-dependence in herring in both sides of the Atlantic occur. Nikolski et al. (1973) claimed that among species with considerable fluctuations in abundance, such as Atlantic herring, the direct relation between fecundity of parent stock and brood strength may be obscured by fluctuations in the survival of young fish under different conditions. They also claimed that fluctuations in abundance are not a passive response to changing environmental conditions, but are an active adaptation of a population's fecundity and the quality of the reproductive products it produces; the adaptation being achieved through changes in the reproduction pattern of the population.

GENERAL DISCUSSION

Fishery biologists have been speculating on the mechanism of fish recruitment and population regulation for a long time. From the fishery management viewpoint, the biologist is expected to maximize fish exploitation without the risk of recruitment failure or possible population collapse. This

question is particularly critical when dealing with a pelagic species such as Atlantic herring which are known for their high variability from year to year in recruitment levels (Anthony and Fogarty 1985). Starting from the premise that there is no apparent correlation between 4T herring stock size and subsequent recruitment (Figure 16), the obvious question is "How are herring populations regulated and at what stage their recruitment established?"

Attempts to answer this question have been made by several investigators. Ideas and hypotheses have been put forward in reference to recruitment mechanisms of Gulf of St. Lawrence herring (Sutcliffe et al. 1977; Winters 1976; Lett and Kohler 1976; Skud 1982; Iles and Sinclair 1982; Sinclair et al. 1985; Koslow 1985). Also, investigations were conducted on factors affecting spawning success and production that have direct or indirect influence on Gulf herring recruitment. For example, effect of temperature on the time of herring arrival on the spawning ground (Messieh 1977); reproductive strategy and larval cohorts (Lambert 1984, Lambert and Ware 1984); density-dependence in population fecundity (Messieh et al. 1985). Nevertheless, the herring recruitment problem remains an outstanding issue and lots of questions are still unanswered.

Templeman (1965) was probably the first to investigate in details the effect of environmental conditions on fish catch and year-class strength in the Gulf of St. Lawrence. He examined several stocks of cod, haddock and herring between 1902 and 1962. In many years, he found good year-classes are common. Moreover, he found two outstanding year-classes were common to herring and cod. It was concluded that the year-class strength must be determined by causes which are pervasive on an oceanic scale. Sutcliffe (1973) and Sutcliffe et al. (1977) found correlations between catches (or year-class strength) and the runoff from St. Lawrence River. They suggested that the river run-off favours primary production and subsequently fish year-class strength. Koslow (1985) on the other hand, argued that large-scale physical processes appear most likely to be ultimately responsible for the observed correlations in recruitment. His argument was based on the fact that good correlation was found between cod recruitment in west Greenland, and recruitment to cod stocks along the North American coast although freshwater outflow contributes to 2% only of the volume of the Labrador Shelf water. Koslow performed a partial regression analysis to demonstrate that the contribution of the salinity at OWS Bravo (station in the center of the Labrador Sea) was three times greater than for St. Lawrence River outflow).

Winters (1976) analyzed the variations in recruitment of 4T herring with changes in stock biomass estimated by cohort analysis. He also studied the variations in herring recruitment with changes in mackerel biomass (Figure 14). Winters indicated that both biomass and population fecundity were reduced to low levels in the late 1950's following a wide-spread of disease in the mid 1950's. As a result of two strong year-classes in the late 1950's, abundance increased dramatically up to 1964 but has declined continuously since then due mainly to subsequent poor recruitment. Mackerel were also at low levels of abundance in the late 1950's and remained so until the mid-1960's when a series of strong year-classes produced a rapid increase in abundance to the extent that mackerel replaced herring as the dominant pelagic fish in the southern Gulf. Density-dependent changes in herring recruitment, growth and maturation rates in relation to changes in herring biomass and total pelagic (herring + mackerel) biomass were shown. Winters hypothesized that the carrying capacity of the southern Gulf for pelagic fish is limited and that competition and predation by mackerel intensifies the logistic response of herring. Thus, recruitment of southern Gulf herring was largely controlled by the total pelagic biomass, acting mainly through herring up to the mid-1960's and through mackerel since then. It was shown also that the increase in mackerel abundance was attributed to a combination of favorable temperature regime and optimum spawning biomass.

Lett and Kohler (1976) investigated the same problem as Winters (1976), but took a different approach. They developed a stochastic model to study effects of temperature perturbations, predation, and competition from Atlantic mackerel on the recruitment process for Gulf of St. Lawrence herring. They concluded that temperature and the abundance of age-group 0 mackerel affected the herring growth rate, but neither total herring biomass nor total pelagic biomass had any measurable effect on herring growth rate. The latter, coupled with adult stock size and environmental effects, mediated through temperature were the prime determinants of larval abundance. Their analysis showed that first-year growth (l_1) of Gulf herring is inversely related to year-class size and act to control population fecundity through effects on subsequent growth and maturation rates.

Winters et al. (1977) disagreed with Lett and Kohler (1976) conclusions re the density-dependence of L_1 and claimed that Lett and Kohler have misinterpreted Messieh's (1973) growth data. This misinterpretation resulted in the assignment of fall spawner year-classes two years too recent and spring spawner one year too recent. When they replotted the data, there was little evidence to suggest a density-dependent relationship between year-class size and first-year growth.

Anthony and Fogarty (1985), however, found indication for density-dependent growth of herring in the Gulf of Maine region. 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 (or other factors indicated by temperature).

Skud (1982) looked into the relationship between Gulf herring abundance and Atlantic mackerel abundance in light of the environmental variations and changes in population 'dominance'. Atlantic herring and Atlantic mackerel have alternated as dominant and subordinate in the pelagic biomass of New England and the Canadian Maritime Provinces for a number of years. The species are known to compete for some food resources and are cannibalistic. Further, the juvenile and adult stages of both species prey on larvae and postlarvae of the other species, so that the role of prey and predator changes with increasing size. Skud concluded that changes in abundance of dominant species of fish were positively correlated with environmental factors that improved survival, and abundance of the subordinate species was negatively correlated with the same factors. When dominance changed, the responses of both the dominant and subordinate species also changed. Implicit in this inverse relation is the conclusion that the abundance of the subordinate depends on the density of the dominant species, and this hierarchy must be recognized in the interpretation of the correlations. Changes in dominance not only explained why the response of a species changed from positive to negative, but also why different stocks did not respond in the same way to temperature.

Skud's hypothesis appears applicable to the Gulf of St. Lawrence herring/mackerel where the relation of temperature to recruit herring was negative from 1963 to 1967. Dominance changed afterwards, and the correlation was positive after 1967. This hypothesis appears applicable also for competing groups within a stock, such as competition between the spring and fall spawning stocks of herring in the Gulf of St. Lawrence. Based on this hypothesis, it would appear difficult to dismiss or accept any of the correlations between recruitment and environmental variations presented in the aforementioned studies, without taking into consideration the dominance of species in question for the period of investigation. Changes in biomass of cod, mackerel and herring, where a predator-prey relationship usually inferred, are shown in Figure 18.

Results of influence of temperature on the time of Gulf herring arrival on the spawning grounds appear to gain general acceptance (e.g. Hay, 1985 for Pacific herring; Cushing, 1982 for several stocks in East Atlantic; Berenbeim and Sigaeu, 1977 for Georges Bank herring). Messieh (1977) and Messieh and Moore (1979) showed that cold years were correlated with late arrival of herring stocks on the spawning grounds, whereas warm years were correlated with early arrival. However, Ware (1979) attempted to nullify the temperature hypothesis on the basis that correlations of temperatures with herring arrivals in some areas were not statistically significant. Unfortunately, Ware's analysis was based on calculation of date of arrival from catch statistics in landing ports far away from the true catch locations. Moreover, he did not distinguish between landings of spawning fish and feeding fish. Hence, the data which he used were not adequate to test the temperature hypothesis.

The difference in the influence of time of spawning within season between spring- and autumn-spawning populations could be explained by their differences in bioenergetics. Although paucity of data impose limitations on any conclusive evidence, Kerr and Dickie (1985) proposed a preliminary bioenergetic model for Gulf herring. From examining their data it was clear that their samples were drawn from summer/autumn-spawned larvae of mean length about 7 mm. Spring-spawned larvae would be about 30 mm at this time. This bioenergetic model suggests that the earliest cohort, detected in the net samples by mid-July, appears to be at a disadvantage over its seasonal history. That is, despite its early start and consequently larger initial body size, the slope of the line of its metabolic realization remains lower than that of the succeeding larval cohort. This could explain the relatively small summer-

spawning population compared to that of spring- and autumn-spawning populations (Lambert, 1984; Lambert and Ware, 1984). Later seasonal cohorts show a much more rapid rise in realization of their metabolic niche potential despite falling water temperatures from August on.

The hypothesis of the role of intermediate cold layer in regulating the timing of herring spring migration from deeper waters offers a plausible explanation for the correlations between herring arrival on Magdalen Shallows and temperature. The short-term effect of temperature in this case is providing a directional cue for triggering the spring migration. A worth noting point is that spring-migrating herring are not all spring-spawners - they comprise both spring- and autumn-spawning populations. That is, the influence of temperature at this stage is to direct the migrating schools to either the spawning grounds (spring-spawners) or to the feeding grounds (autumn-spawners) which, in this case, coincide on the Magdalen Shallows.

The Magdalen Shallows in relation to the Magdalen Shelf and the Laurentian Channel provide oceanographic characteristics peculiar to the Gulf (Trites 19). Environmental conditions on the Magdalen Shallows are mainly influenced by St. Lawrence River runoff, wind and temperature, which are all interrelated. The seasonal changes in the size of the intermediate cold layer is an annual regular event, subject to year-to-year variations, which would explain the yearly variation in the timing of herring arrival. Unusual environmental conditions like those of the prevailing tropical storms in April 1958 occur, and these would result in unusual strong year-class.

The erratic variations in temperatures on the spawning grounds, which resulted in mass mortalities of herring eggs on Fisherman's Bank spawning ground in September 1985, appear to be a common phenomenon on the Magdalen Shallows. Drinkwater (pers. comm.) described a similar phenomenon in St. Georges Bay. The response of herring populations to this diverse environmental conditions could explain the multiplicity of the herring spawning grounds as an adaptive reproductive strategy. That is, herring have learned not to put all their eggs in one basket. It appears difficult that one spawning population can repopulate another, as hypothesized by Sinclair and Iles (1981) and Iles and Sinclair (1982). In this hypothesis both the existence and the mean size of spawning populations are postulated to be a function of the existence of geographically fixed larval retention areas. Larval cohorts of herring appear to be a general phenomenon (Lambert, 1984). Messieh and MacDougall (1984) showed the larval distribution in two successive cruises (2 weeks apart). Messieh (unpublished data) showed that areas where larval cohorts appeared are characterized by a combination of cyclonic gyres (a type which has tendency to disperse larvae) and adjacent anticyclonic gyres (a type which has tendency to retain larvae). The role of these gyres on larval ecology and subsequent recruitment would require further investigation.

In the foregoing discussion, the influence of environmental conditions on herring production and recruitment in 4T area is emphasized. This should not undermine the effect of other biological interactions on recruitment which may occur throughout the life history of fish. Indeed, density-dependent population fecundity has been demonstrated for Gulf herring (Messieh et al. 1985). A reasonable explanation for the observed increase in fecundities in recent years is the decline in abundance of herring.

There is nevertheless a paradox. Growth rates at age for adult herring have been reported to increase with increasing population abundance. This suggests that food is not limiting, for adult growth at least, over a wide range in abundance. Yet at the drastically reduced spawning population size observed in recent years there is evidence of increased fecundity. Given the lack of food limitation inferred for adult 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 availability of energy.

The predation on herring eggs by an array of predators must have a substantial impact on egg survival. In discussing the relationship between Atlantic mackerel and Atlantic herring, there was no previous reports on predation on herring eggs by Atlantic mackerel. To my knowledge, this was the first time direct observation by SCUBA divers, schools of Atlantic mackerel (pelagic feeder) were seen actively feeding on herring eggs (demersal). Accepting the role of the effect of environmental changes on recruitment variability of 4T herring, one might wonder if there is any sense in controlling fishing effort on herring fisheries. Anthony and Fogarty (1985) reported that the greatest fluctuations in recruitment of Gulf of Maine herring, historically, occurred in the absence of high fishing mortality.

They showed that recruitment since 1947 has varied by a ratio of 20 to 1. Since heavy fishing began in the mid-1960's, recruitment has fluctuated by only a factor of 9 to 1. Jones (1982), and Doubleday (1985) showed the possible consequences of changes in fishing effort associated with changes in recruitment due to environmental variation. If fishing effort and recruitment were relatively low, and recruitment improves - unknowingly - due to environmental change, the immediate effect is an increase in stock size and recruitment. If, in response to this, there is an increase in fishing effort, a drastic decline or even a collapse of the stock may occur, if environmental changes return to the previous conditions (Figure 19). Pelagic stocks appear to be much more vulnerable than demersal stocks, and this would explain what has happened to many pelagic fish stocks, when subject to environmental change as well as heavy fishing. Recent examples of stock collapses are Georges Bank herring stock and Magdalen Islands stock.

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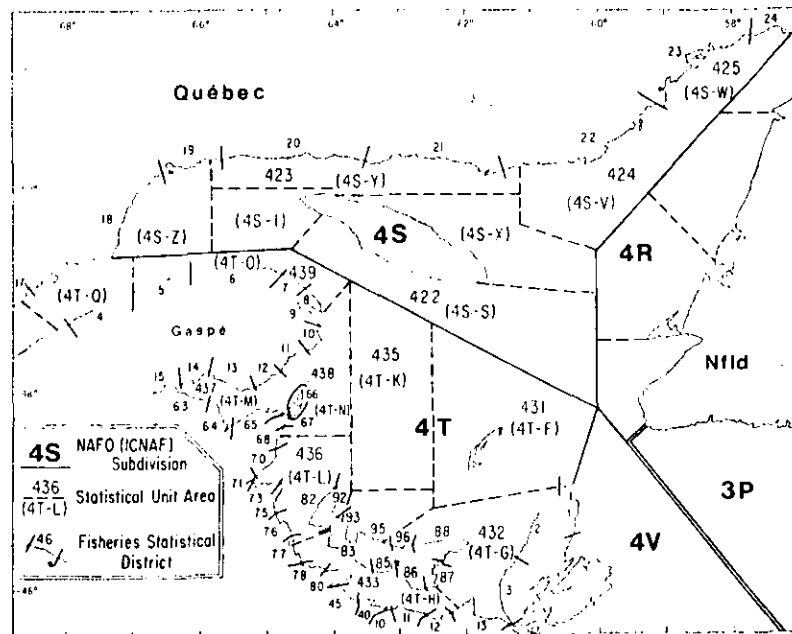


Figure 1. Gulf of St. Lawrence showing Fishery Districts and NAFO Divisions.

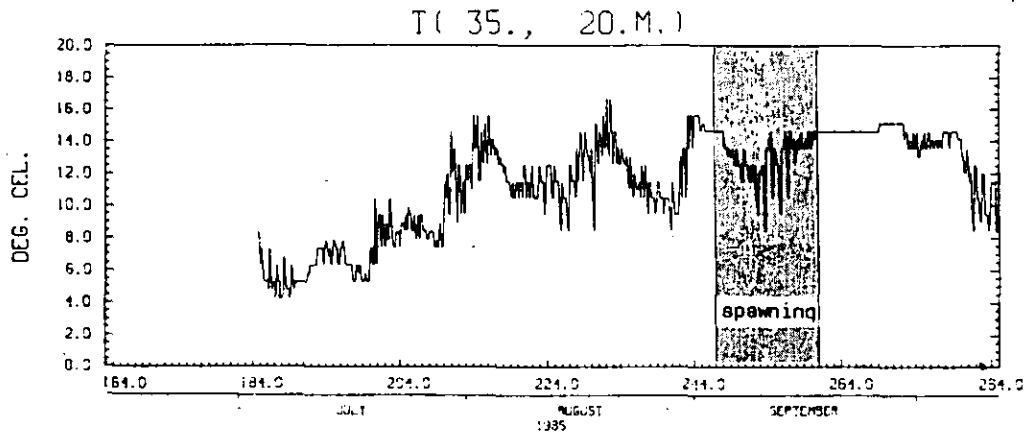


Figure 2. Ryan thermograph record showing variations in temperatures at 20 m from July to September 1985.

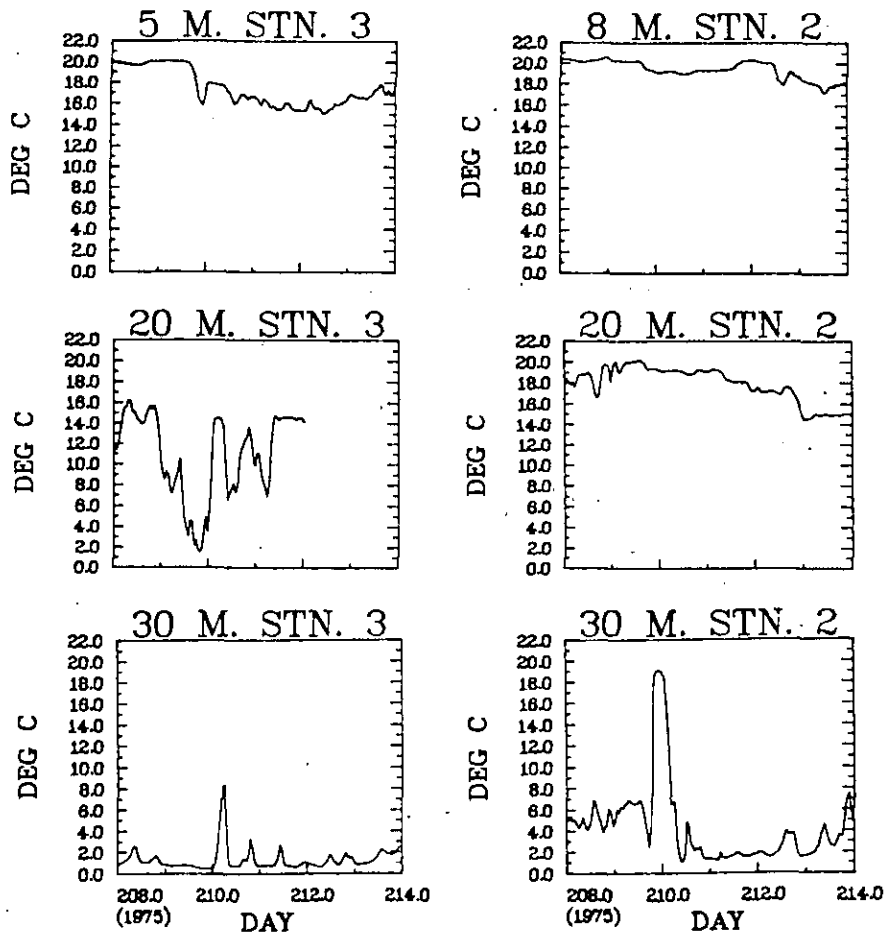


Figure 3. Temperatures at 2 stations in St. Georges Bay from July 27 (day 208) to August 2 (day 214). Note that while no striking change in temperature was observed near the surface, at 20 m and 30 m, changes of over 10°C occurred (Drinkwater, unpublished data).

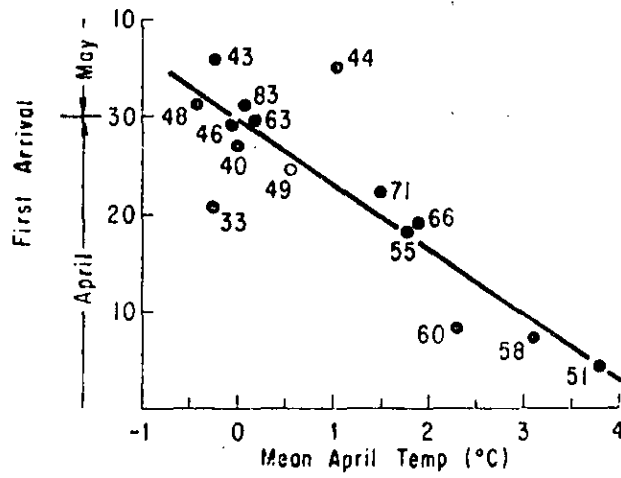


Figure 4. Regression of time of herring arrival near Magdalen Islands spawning ground and mean April's surface temperature.

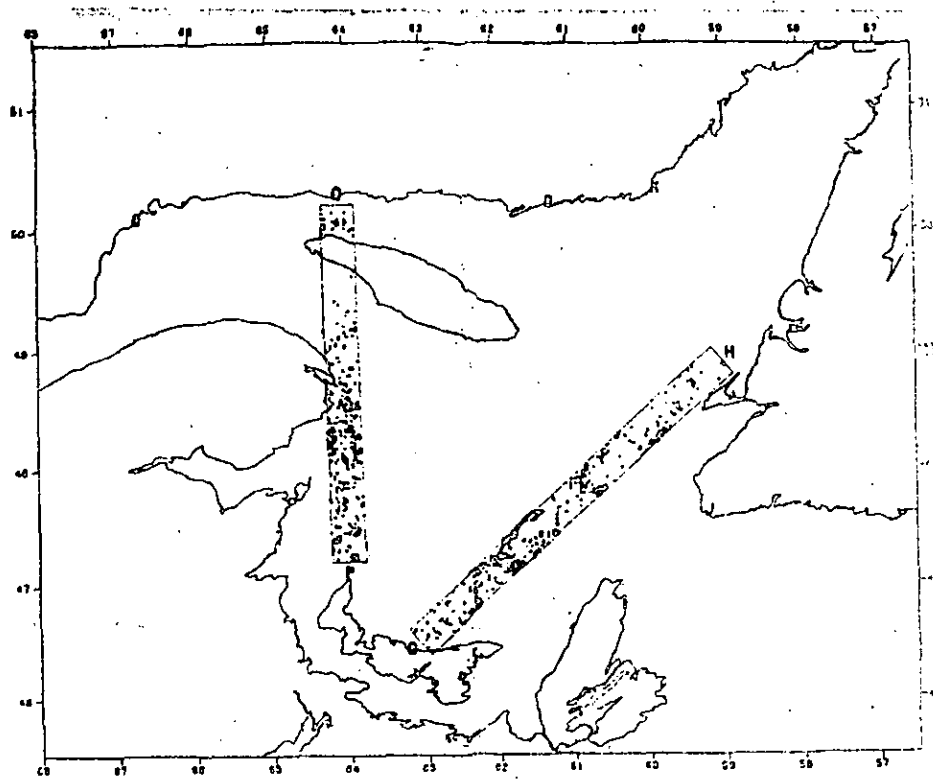


Figure 5. Location of 2 sections showing stations used for vertical temperature distribution analysis.

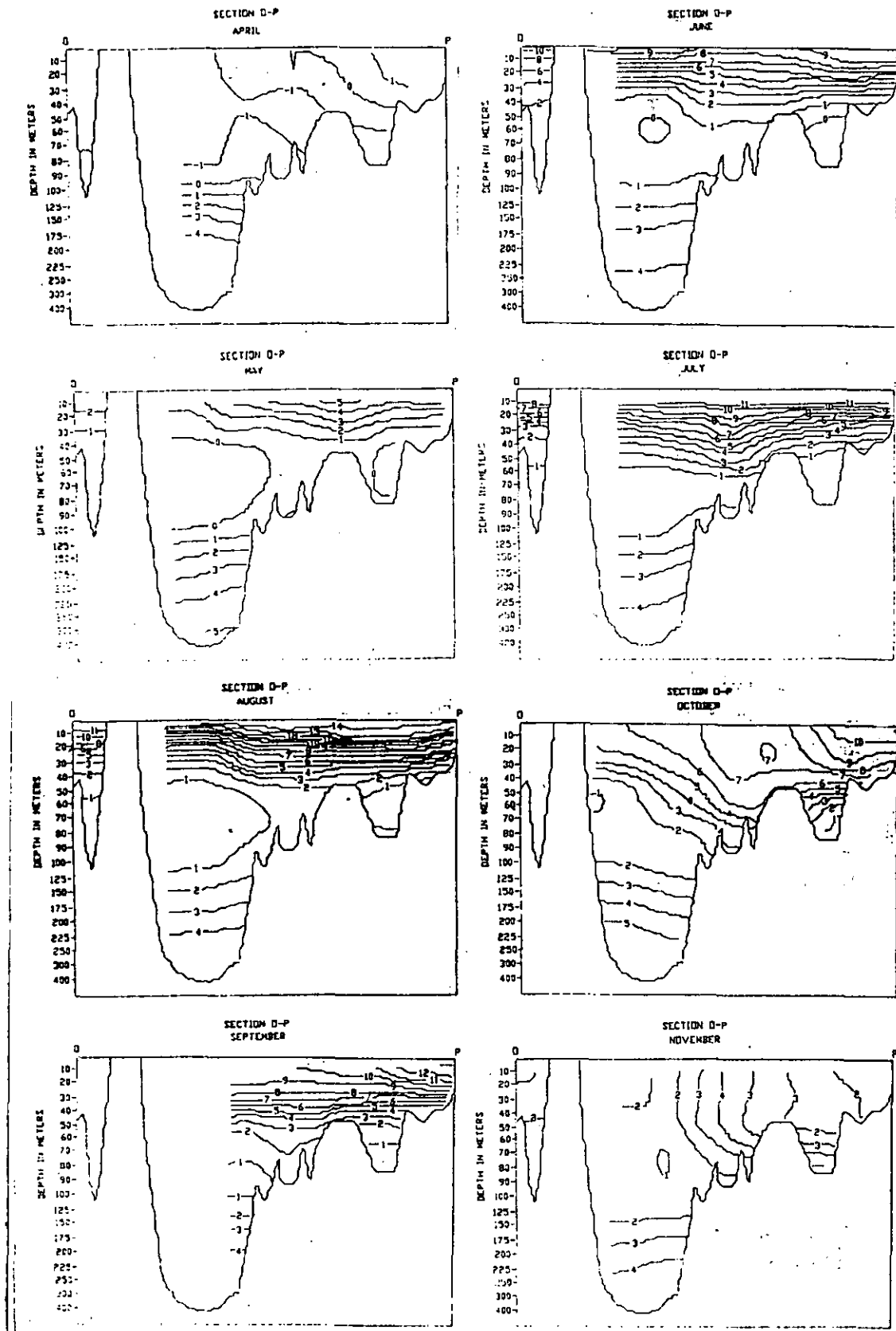


Figure 6. Monthly variations of temperatures from April to November along section O-P showing changes in water stratification.

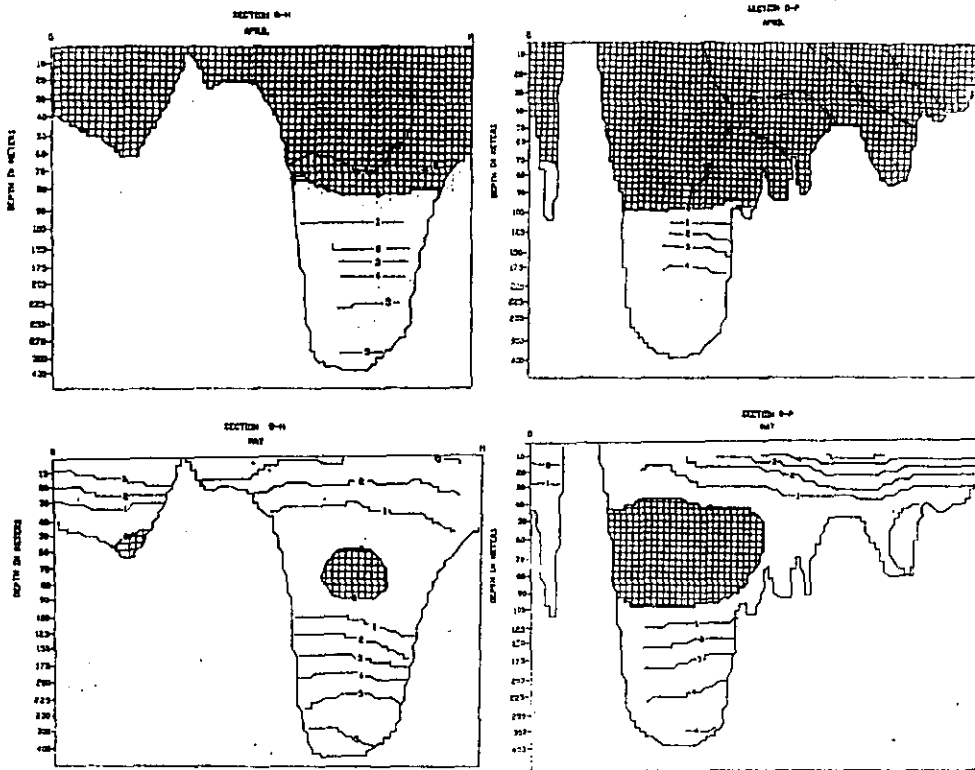


Figure 7. Vertical sections along G-H and D-P showing the change in the intermediate cold layer from April to May.

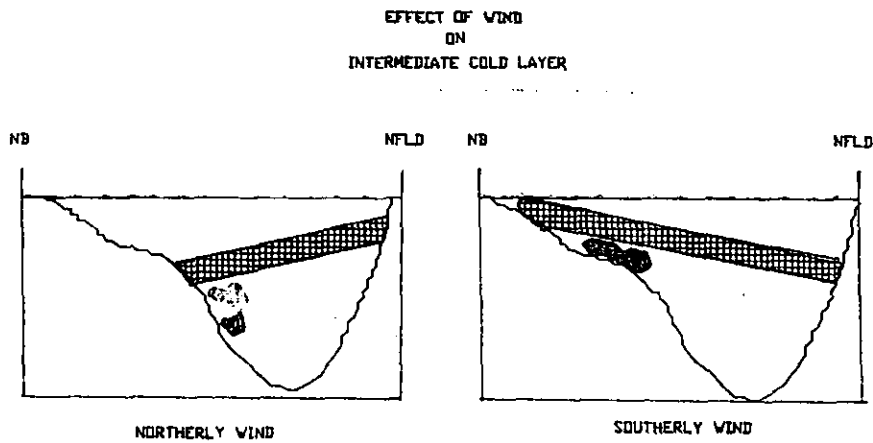


Figure 8. A section across the Laurentian Channel showing the internal adjustment of the cold intermediate layer under the influence of (a) strong northerly winds, and (b) strong southerly winds.

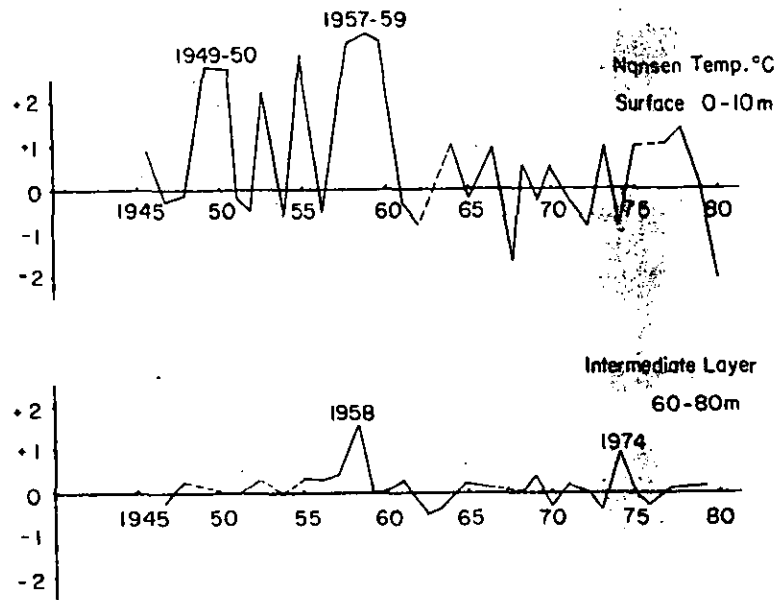


Figure 9. Temperature anomalies in spring in the Gulf of St. Lawrence, 1945-1980 at surface (0-10 m) and intermediate layer (60-80 m).

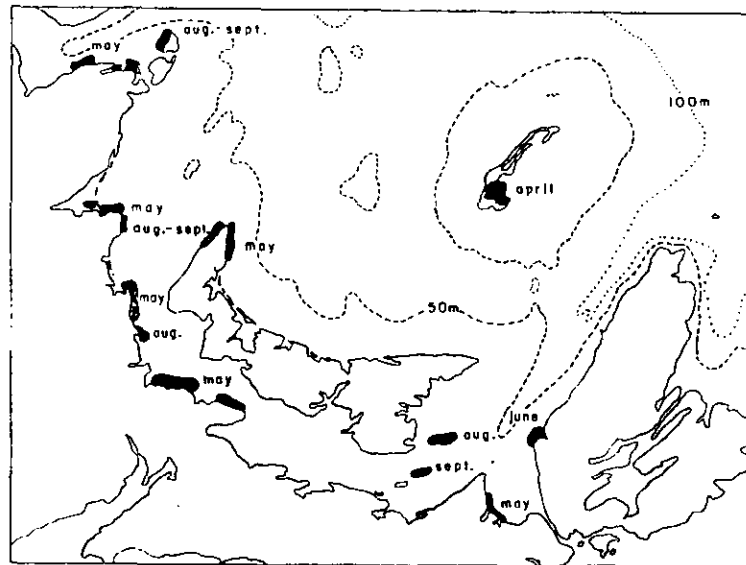


Figure 10. Map of the southern Gulf of St. Lawrence showing the spawning grounds of spring- and autumn-spawning herring.

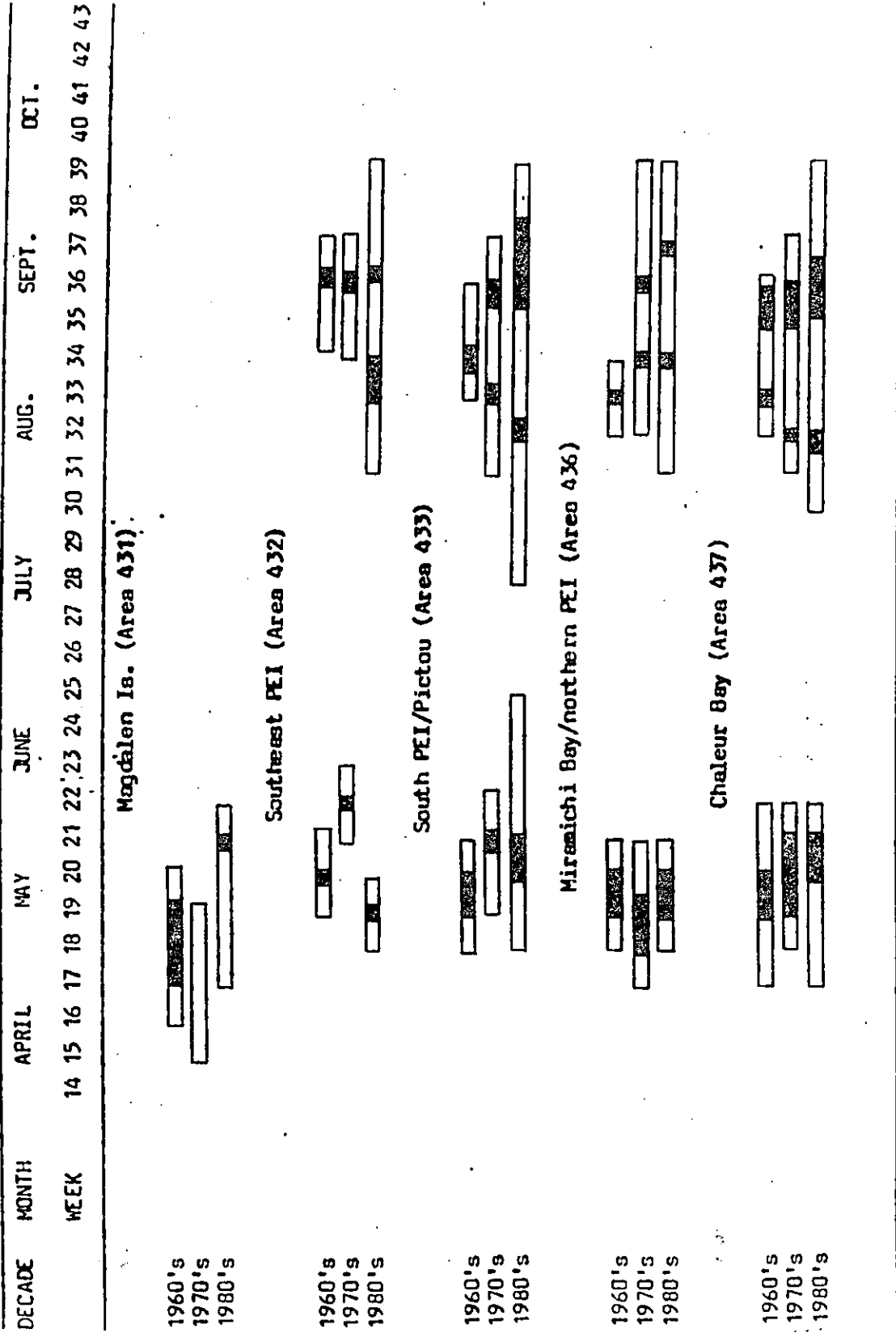
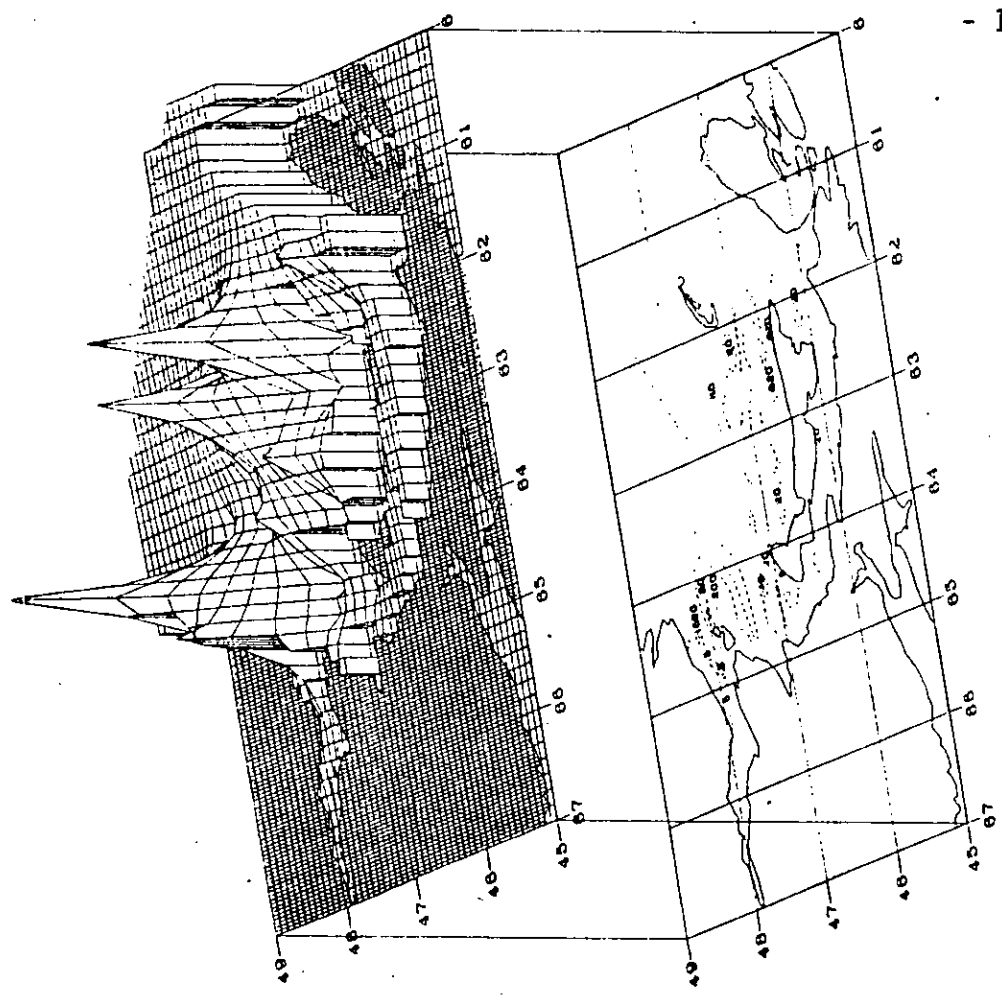
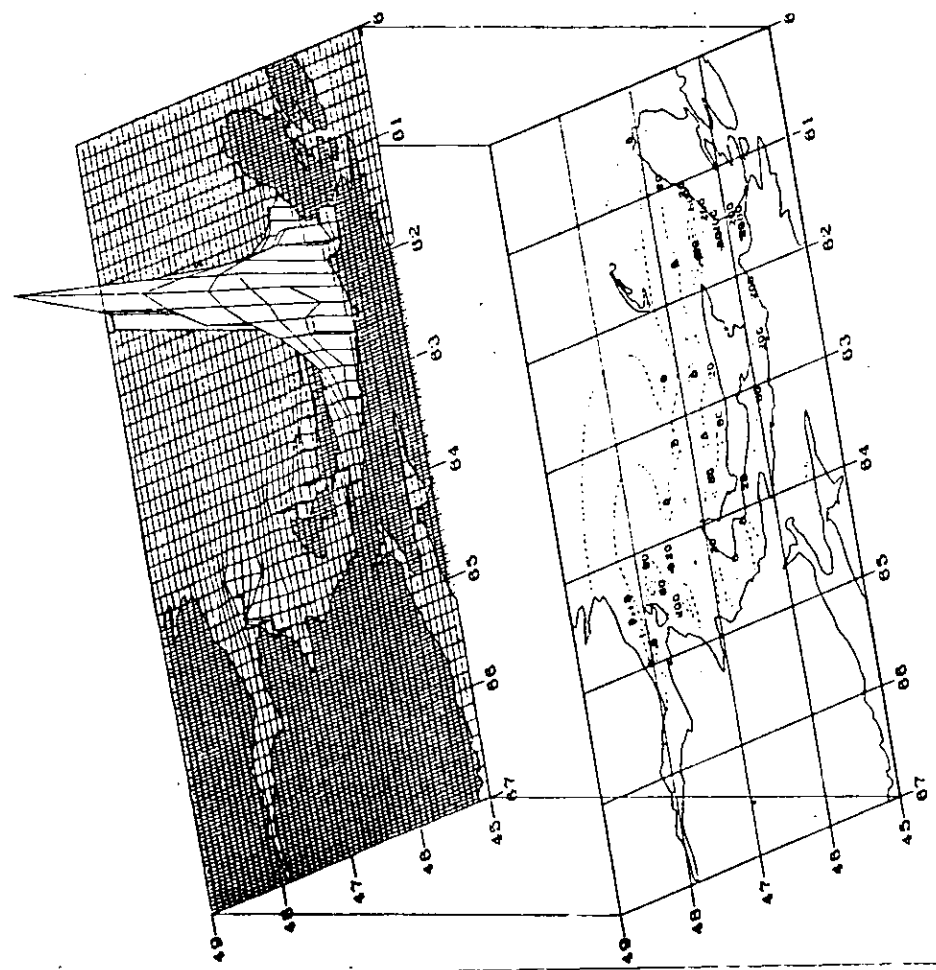


Figure 11. Spawning time of spring- and autumn-spawning herring in 3 decades, showing the range of spawning and peak spawning (>50% ripe and running fish).



M001 Herring Larvae per 10m square Oct. 10 - 14, 1979



M001 Herring Larvae per 10m square Sept. 19 - Oct. 1, 1979

Figure 12. Distribution of herring larvae per 10m² in successive cruises (2 weeks apart) in the southern Gulf of St. Lawrence.

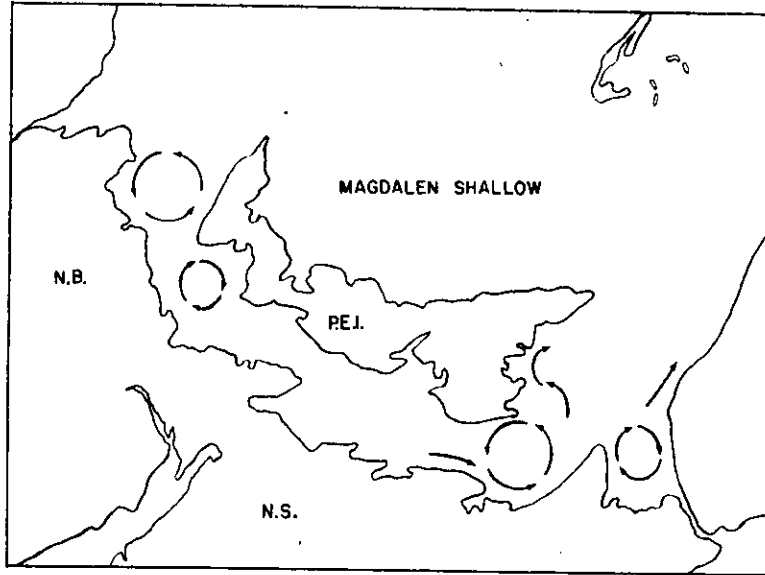


Figure 13. Map of southern Gulf of St. Lawrence showing two locations near herring spawning grounds where cyclonic and anticyclonic gyres usually occur.

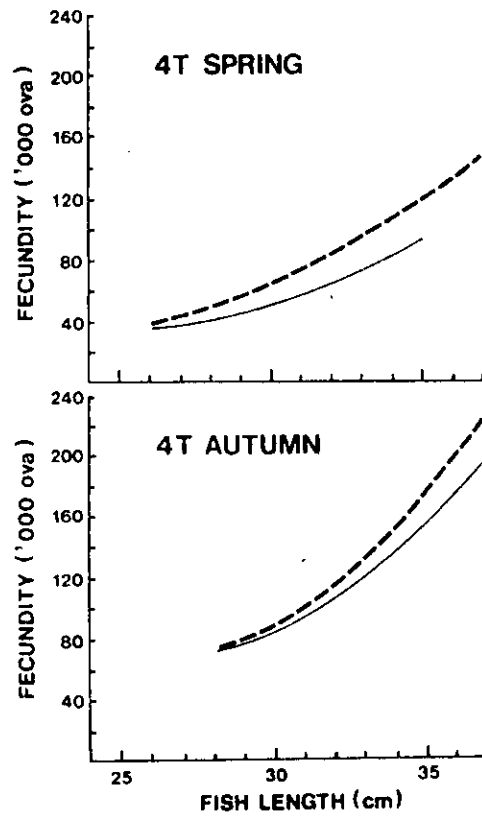


Figure 14. Regression of herring fecundities on fish length before and after 1973.

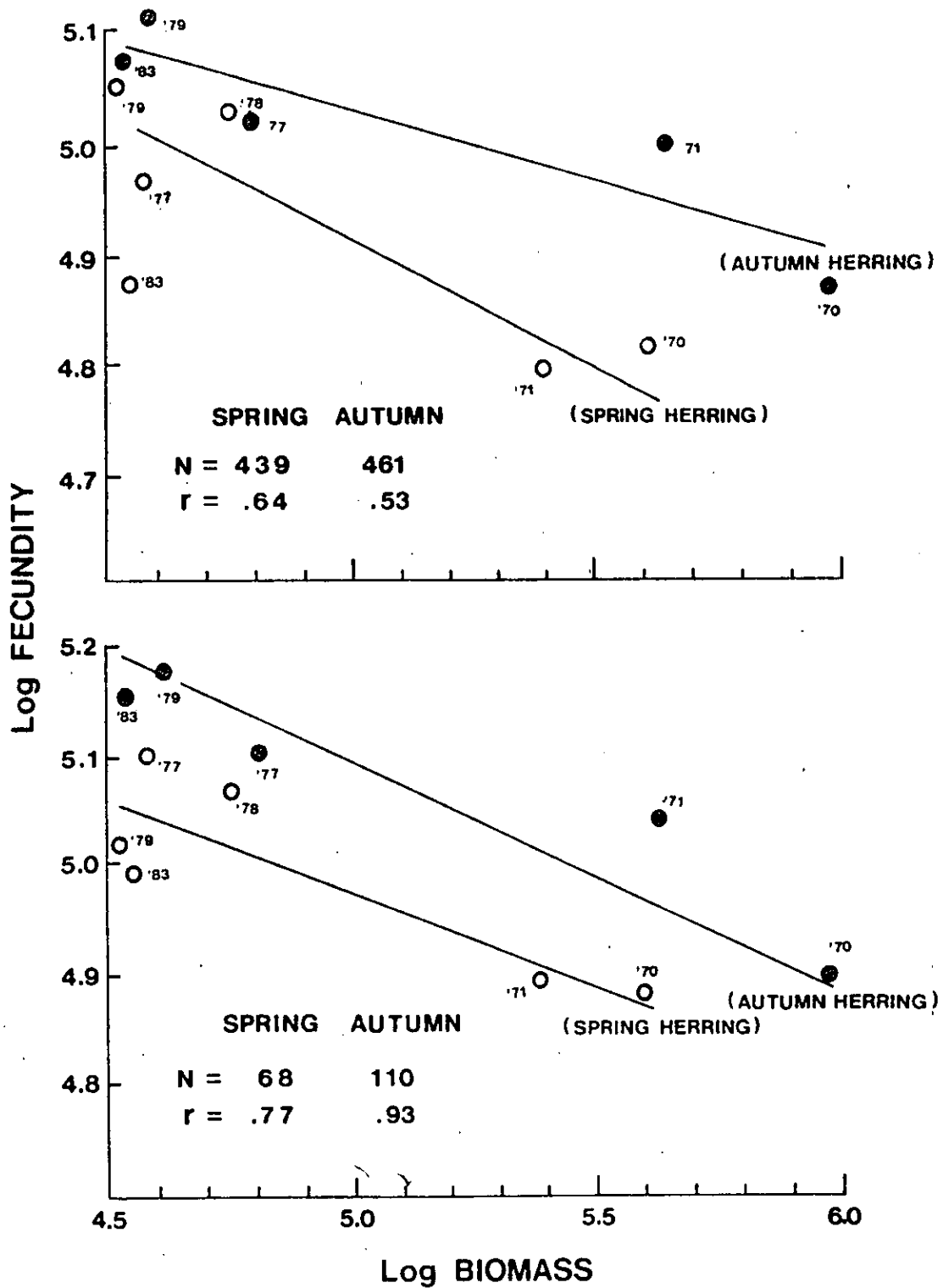


Figure 15. Regression of herring fecundities or biomass (a) for all sizes combined and (b) for dominant size group.

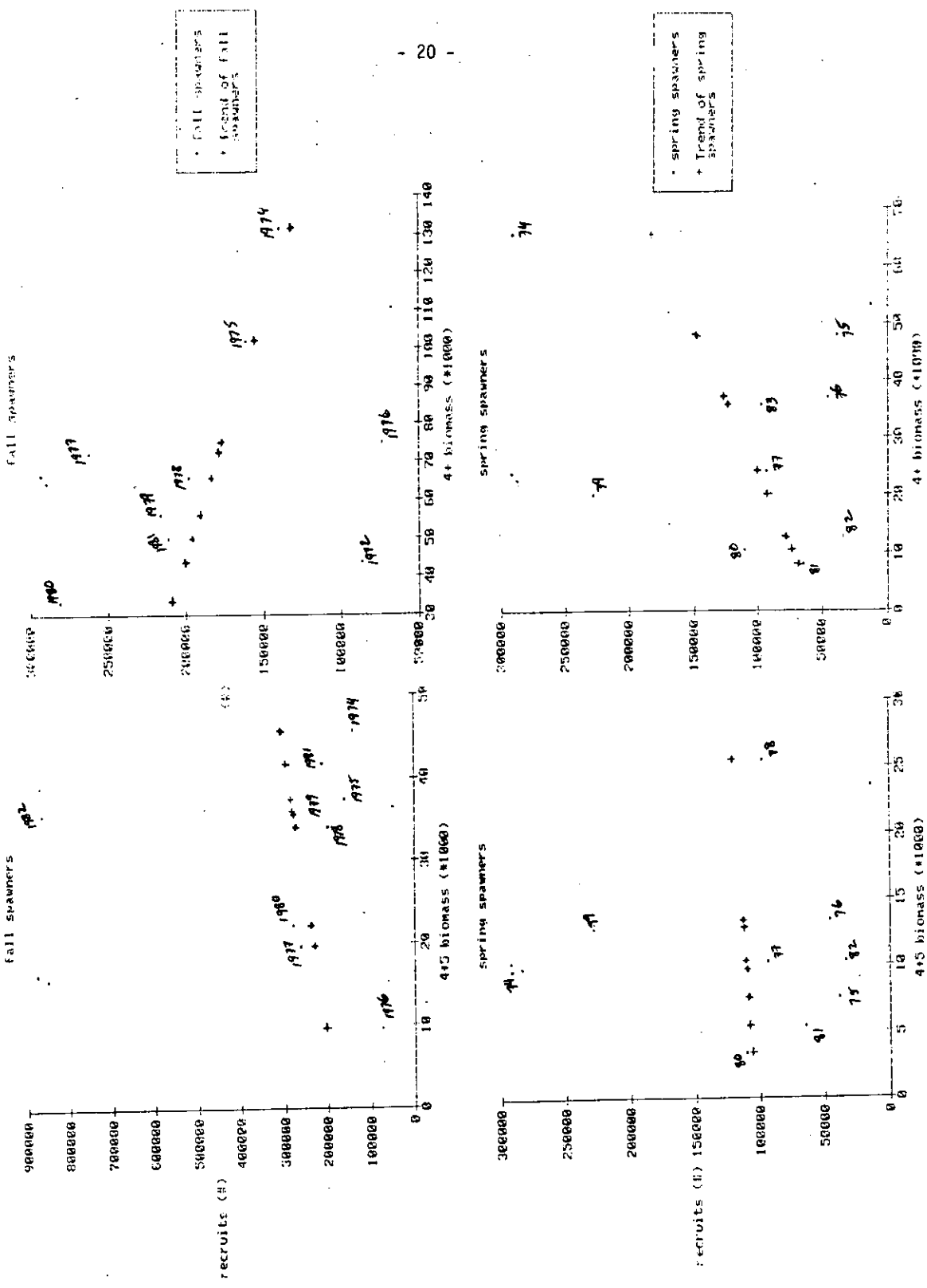


Figure 16. Relationship between herring recruitment and stock biomass.

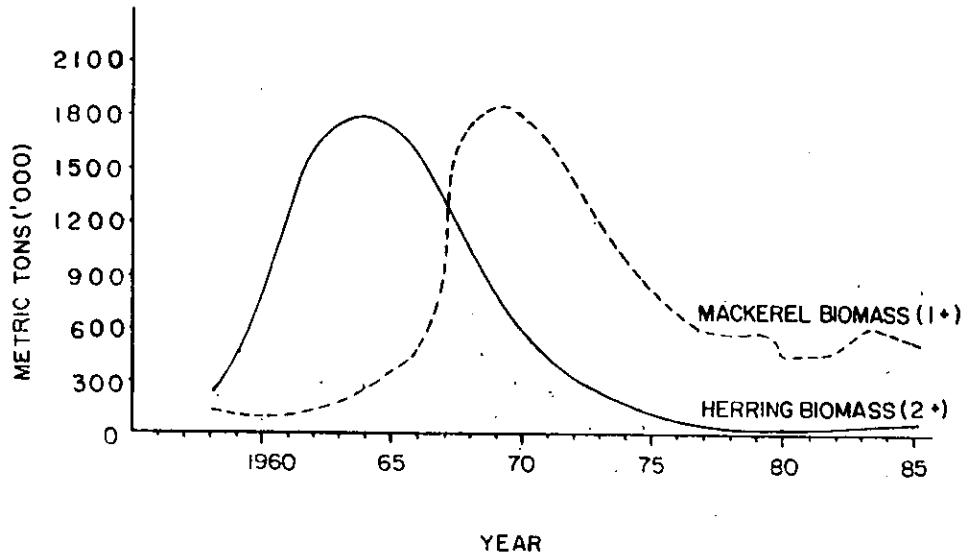


Figure 17. Changes in herring and mackerel biomass, 1958-1985.

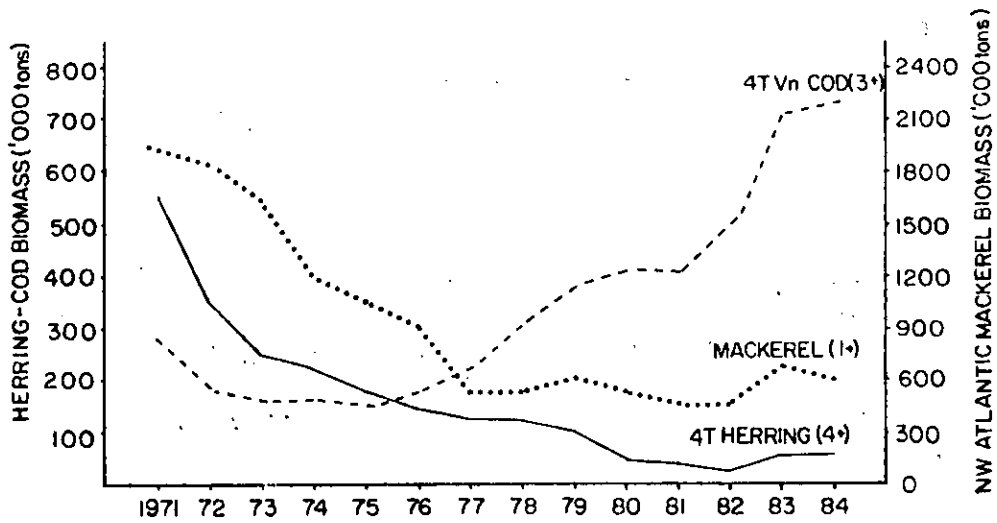


Figure 18. Biomass of herring, cod and mackerel, 1971-1984.

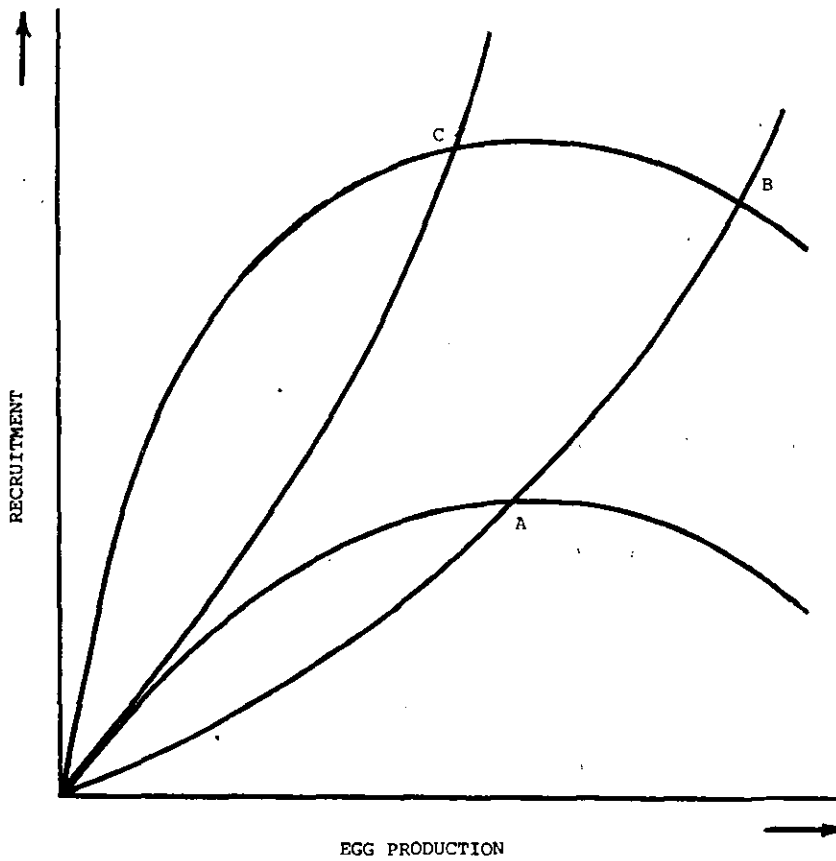


Figure 19. A theoretical illustration of the relationship between egg production and subsequent recruitment for a pelagic species, showing possible stock collapse if a sustained increase in fishing effort follows a temporary improvement of recruitment resulting from unusual favourable environmental conditions, as those prevailed in 1958-59.