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A model of the interactions of temperature with the recruitment
mechanism for the Gulf of St. Lawrence cod stock¹

by

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Abstract

A multivariate approach was used to elucidate the simultaneous effects of the environment and estimated stock biomass on the recruitment of Gulf of St. Lawrence cod. The quadratic effects of temperature and estimated stock biomass were key factors in determining egg abundance levels. The numbers of larvae were found to increase linearly with egg abundance and temperature. A distinct dome shaped density-dependent relationship existed between the numbers of larvae and the estimated abundance of 2+ cod. A simplistic simulation, constructed to test the behavior and validity of the derived equations, showed year-class strength for cod could be predicted 4 years in advance of their recruitment into the fishery. The addition of a fishery sub-model produced regular 12-yr oscillations in stock size, the amplitude of which depended on the fishing mortality.

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Introduction

Historically, fisheries biologists, guided by such forerunners as Beverton and Holt (1957) and Ricker (1958), have rigorously studied the response of fish populations to exploitation, assuming constant recruitment independent of environmental effects. However, it has also been realized that the environment does play an important role in determining recruitment but the mechanism remains to be elucidated. In the light of the accepted importance placed upon these effects, egg and larval surveys were initiated in the southern Gulf of St. Lawrence to try to link up environmental effects on recruitment with those due to fluctuations in parent stock biomass. In addition, it was anticipated that some important insight could be gained concerning groundfish egg and larval biology.

That temperature is an important environmental factor regulating cod production is demonstrated by the positive correlation between temperature and cod abundance at the northern limits of their range, while a negative relation is found at the southern limits (Dickson and Lamb 1973; Templeman 1973). This effect was shown at West Greenland (Hermann 1953; Hermann et al. 1965), at Labrador (Elizarov 1965), in the Norwegian and Barents Seas (Kislyokov 1961), off Nova Scotia and New England (Martin and Kohler 1965), in the North Sea (Holden 1970), and in the English Channel (Dickson and Lamb 1973). More recently W.H. Sutcliffe, Jr. (personal communication) found a negative correlation between temperature and cod catches in the Georges Bank and Scotian Shelf area.

It is the aim of this paper to analyze the effect of the interaction of temperature, as the key environmental factor, with parent stock biomass in determining the stock recruitment mechanism for cod. Furthermore, an attempt is made to construct a model to predict recruitment as well as to elucidate the long-term effects of exploitation.

Methods

In 1965 an investigation of the distribution and abundance of fish eggs and larvae in the southern Gulf of St. Lawrence was initiated and subsequently continued until 1972. Examples of the cruise tracks and plankton-towing stations are shown in Figure 1. For the present analysis only the samples from two types of nets were considered, standard conical meter nets and Miller samplers (Kohler et al. 1974). The conical meter nets were 10½ ft long and were constructed of No. 471 Nitex nylon. The Miller samplers were constructed using plans made available by U.S.F.W.S., Woods Hole, Massachusetts. Volumes of water strained by the standard conical meter nets were measured with TSK flow-meters (Tsurumi-Seiki Kosakusho Co. Ltd., Yokohama, Japan). The conical meter nets (surface and 15 m), stacked on a wire at various depths, were towed simultaneously at 2½ knots, each for half an hour. The ships used for these cruises were the M.V. *Harengus* and C.G.S. *E.E. Prince* and *A.T. Cameron*.

The nets were thoroughly washed down with salt water when brought aboard after towing. Samples were routinely stored in 32-oz glass bottles. Special effort was made in the identification of eggs and larvae between 1965 and 1972. Sometimes it was almost impossible to differentiate between eggs of Atlantic cod and other gadoid species; however, larvae could be separated by their irregularities in pigmentation (Bigelow and Schroeder 1953). When there was any doubt concerning the species to which the eggs belonged, they were incubated and the hatched larvae subsequently identified.

Preliminary data analysis

Some amalgamation of the large amounts of data collected between 1965 and 1972 was necessary before any analysis was possible. The strong auto-correlation between successive tows within a cruise indicated the best method to

observe unbiased patterns within the data was to treat an entire cruise as one experimental unit. The analysis of the data could then be treated as a multiple split plot design (Cochran and Cox 1968) with cruises being the main plot. The first split within cruises was a breakdown of gear types, all adjusted to a constant amount of water strained (100,000 cu m); thus catches of the largest gear type, the 6-ft Isaacs-Kidd trawl, were reduced and the catches of the smaller Miller samplers were increased. Those with a different mesh size in the codend (#471 Nitex) were not used in the analysis. Calculated flows on the meter nets did not differ from the observed flows taken by the TSK flow-meter by more than 5%. This level of accuracy was assumed to apply to the calculated flows for the other nets. The next split, within gear, was depth.

Preliminary analysis of the gear types showed that adjusted egg and larvae catches for Miller samplers and one-meter nets were not significantly different. Catches in the other types of gear were an order of magnitude lower than these, and were not comparable. Depth was not found to be significant in determining egg availability, therefore, tows at different depths were used as an estimate of pure error (Draper and Smith 1966). However, the number of larvae caught in surface nets was significantly lower than catches at other depths, thus only catches at depths other than the surface were used. The changing intensity of the surveys presented a considerable problem (Appendix 1) which was overcome by giving more weight in the analysis to those years with a more intense survey. The mean sea surface temperatures were calculated for each depth and gear type while a mean salinity was used for an entire cruise.

Results

Derivation of equations

Temperature and stock size were found to be major factors affecting the catch of cod eggs by survey vessels during May (Fig. 2). The general relationships among these variables were described by the following multivariate relationship:

$$(1) E_g = 11.6303B - 5.3270B^2 + 0.0297T_p^2 - 0.0039T_m^2 - 2.4256$$

Variable	Coeff.	Student 's t	Partial Corr. Coeff.
B	11.6303	2.01 ^a	0.3730
B ²	-5.3270	2.98 ^a	-0.5119
T _p ²	0.0297	2.27 ^a	0.4131
T _m ²	0.0039	7.80 ^a	-0.8347

^aSignificant at P<0.05

The coefficient of multiple determination (R²) was 0.830 while the F for regression was 18.16^a. E_g is the catch of eggs/1000 cu m of water strained, and B is the estimated stock biomass on May 1st for sexually mature individuals 4 years and older (Appendix 2). Virtual population analysis (Pope 1972) was used to estimate the numbers of cod in the parent population on January 1st. The number of fish caught between January and May in ICNAF subdivisions 4T and 4V_n and number of cod lost to natural mortality (m = 0.20) were subtracted from the January 1st estimate to give the size of the spawning population. Mean weights for each age in May were determined from commercial sampling and multiplied by the numbers to give parent stock biomass. T_p is the mean sea temperature during the cruise; T_m is the median time of the cruise after May 1st.

Equation 1 can be reduced to a form involving only temperature and stock biomass given values for time. On the 30th May the equation reduces to the following form:

$$(2) E_g = 11.6303B - 5.3270B^2 + 0.0297T_p^2 - 5.9356$$

However, the equation and graph depicted in Figure 2 represent the reduced form of equation 1 on May 20th. The time-dependent term demonstrates ^{that} egg mortality is quadratic and generated over time independent of the estimated stock biomass and temperature. The effects of this time-dependent term are quite profound: On May 15 the predicted catch of eggs/1000 cu m of water strained is 3.1 (for 5 C and estimated stock biomass of 1.2×10^5 metric tons) while, by May 30, it has fallen to 0.5.

The quadratic nature of parent stock biomass (equation 1) suggests a density-dependent mechanism is controlling the number of eggs (Fig. 2). The general trend over the data series is a decline in egg numbers with increasing stock biomass. There are a number of possible explanations. However, the analysis suggests that either large estimated parent stock biomasses are producing fewer eggs, or that large numbers of these eggs are dying immediately following spawning, since the mortality generated over time does not interact with parent stock biomass.

The effect of temperature is quadratic, although the coefficient for the temperature is small (0.0297), indicating that it is less important in determining the catch of eggs than estimated parent stock biomass. The exponential effect of temperature is in accord with finds of Forrester and Alderdice (1966) and Bonnet (1939).

The abundance of larvae was found to be positively correlated with the catches of cod eggs in May, and temperature (Fig. 3). The following multivariate equation describes the relationship:

$$(3) L_R = 34.1040E_g + 3.1312T_p - 0.1570E_g \times T_m - 46.8381$$

Variable	Coeff.	Student's t	Partial Reg. Coeff.
E_g	34.1040	3.16 ^a	0.791
T_p	3.1312	1.83 non-sig	0.598
$E_g \times T_m$	-0.1570	1.67 non-sig	-0.562

^aSignificant at $P < 0.05$

The coefficient of multiple determination (R^2) is 0.70 while the F for regression is 4.56 where L_R is catch/100,000 cu m of water strained, E_g is the catch of eggs in May/1000 cu m of water strained, and T_p is the temperature in °C on the time T_m in the days from May 1st. The predictive value of equation 3 is less than equation 1 but both T_p and the $E_g \times T_m$ interaction lead to a substantial decline in the error mean square and subsequently can be considered significant variables (Draper and Smith 1966).

The yearly temperature cycle in the Gulf of St. Lawrence reaches a maximum usually in early August (Lauzier 1969), therefore 100 days was substituted into equation 4 for T_m to approximate the temperature maximum.

$$(4) L_R = 18.4040 E_g + 3.1312 T_p - 46.8381$$

The $E_g \times T_m$ interaction indicates that the importance of egg numbers in determining larval abundance is reduced and dependent on time. However, in equation 3, the effect of time on larval numbers is not profound presumably since the critical period for larval survival was determined earlier in June. Hermann et al. (1965) also found the best correlation between temperature and the numbers of surviving larvae was in June.

A density-dependent relationship exists between larval abundance and the numbers of juveniles, 2 yr later (Fig. 4). The \log_e CUE of 2^+ juveniles was determined by Hare and Kohler (1974) from juvenile surveys in the Gulf of St. Lawrence. The regression of the CUE of 2^+ cod on the abundance of 2^+ cod estimated from virtual population analysis was significant at $P \leq 0.05$. The CUE of 2^+ cod was then assumed to be measured without error and was used to estimate the numbers of 2^+ cod (Appendix 2). Therefore the estimate of numbers at age 2^+ is no more accurate than the CUE from juvenile surveys.

Initially, as the abundance of larvae increases, the

number of juvenile cod increases following a logistic pattern, reaching a maximum near a catch (per 10^5 cu m of water strained) of 12. At catches greater than 12 there is an inverse relationship between larval abundance and numbers of cod at age 2^+ . However, when the catch of larvae is 0, the year-class strength of 2^+ cod is approximately 65×10^6 fish. Presumably, the larval density was too low for individuals to be caught by the survey cruises.

Test of equations using simulation

To test the validity and conservatism of the derived equations in predicting year-class strength, a small deterministic simulation was constructed amalgamating the different portions of the egg, larval and juvenile biology of cod. The exogenous controls on the final prediction of year-class strength from the system of equations were estimated parent stock biomass and the temperature cycle in the Gulf of St. Lawrence. The sea surface temperatures at Grande-Rivière were correlated with those from the cruises and were used for prediction. Sea surface temperatures showed considerable variation among the 12 yr of data considered (Appendix 2). The spring temperatures at Grande-Rivière were considerable above those farther out in the Gulf but the correlation between the two was significant ($r = 0.77$). The correction equation of $Y = 0.57X + 1.67$ was used, where Y is the temperature in the Gulf of St. Lawrence and X was the temperature at Grande-Rivière. Surface temperatures at Grande-Rivière were below Gulf temperatures in late summer and early fall. The correlation between the two was again high ($r = 0.79$) and the correction equation $Y = 1.08X + 0.67$ was used.

Generally, equation 2 was used to predict the catch of cod eggs, notable exceptions being 1963-69. In these two years the equation derived for egg abundance on May 20th approximated the catches more accurately. Possibly, the mortality rate between May 20 and 30 could have been reduced by

these years being particularly calm. Rollefson (1930,1932) suggested wave action can burst yolk membranes and kill eggs; however, meteorological records show no significant drop in the average May wind speed in these 2 yr. In 1968 and 1969 the accumulated growth of cod was at a maximum (Halliday 1972) which has been found to be an important factor in determining egg survival (Grauman 1973). It is possible that improved egg survival could be due to the enhanced condition of cod.

The estimated temperature maximum and egg abundance were used as the dependent variables in equation 4 to estimate the catch of larvae. The relationship between larval abundance and the abundance of age 2⁺ juveniles was approximated by a number of straight lines since no satisfactory fit was obtained using density-dependent and independent mortality curves postulated by Cushing and Harris (1973). A 4-order polynomial would be an adequate fit to the data, but would have no biological meaning.

The correlation between the simulated (predicted) (observed) year-class strengths and those estimated / from juvenile surveys was significant at $P \leq 0.05$ while the line at 45° indicated parity between the two variables (Fig. 5). Furthermore, both the predicted and observed year-class strengths were previously determined using estimates from virtual population analysis. The difference in slope and position of the regression line through the points was not significantly different from the line representing parity. This significant correlation suggests that the derived equations hold over the data series from 1960-1971. However, further tests were made to study the behavior of the predicted values under controlled conditions.

An attempt was made to simulate a Ricker (1954) stock and recruitment relationship for different temperature cycles. No relationship existed between / juveniles at age 2⁺ and parent stock biomass of 0.5×10^5 - 2.5×10^5 metric tons,

nor was there any hint of a gadoid dome (Cushing and Harris 1973) for Gulf of St. Lawrence cod. The scatter of recruitment values was reduced at stock biomasses of approximately 1.5×10^5 metric tons, suggesting this to be the parent stock biomass producing the most consistent recruitment. As the parent stock biomass was reduced the variance in recruitment increased. However, a general decline in recruitment with stock biomass was noted. In light of the simulated results, it appears that the recruitment curve, suggested by Beverton and Holt (1957), with considerable associated variance, best summarized the results. Within the estimated stock biomasses observed in the Gulf of St. Lawrence, a good estimate of recruitment would be the mean of the scatter in the absence of environmental data.

A submodel, representing a hypothetical fishery, was added to the simulation to study the behavior of the equations under different levels of exploitation, and to make the estimated stock biomass an endogenous variable. It was anticipated that the regular 9-12 yr fluctuations, stipulated by Ricker (1954) and observed for gadoids by Grosslein and Hennemuth (1973), could be generated. Iles (1973) also discussed the significance of regular fluctuations in a number of fish stocks and Caddy (MS 1974) noted an 8-9 yr periodicity in the abundance of Bay of Fundy scallops.

This model, including the fisheries submodel, was programmed in C.S.M.P., a computer language particularly suited to the simulation of long-term continuous time-dependent processes. The fisheries submodel was kept as simple as possible, responding only to instantaneous fishing and natural mortality (0.2) (Clayden 1972; Halliday 1972). The same instantaneous rates were applied to all age classes and the partial recruitment of 4-yr-olds was not included. Under present fishing conditions cod become fully recruited at age 5 (Halliday 1972). The simulated

period was 250 yr, although only a portion of the entire period is discussed. The mean weight of individuals in the population and the annual temperature cycle of the Gulf were also held constant.

The simulated results of exploitation profoundly affected stock numbers. As the instantaneous rate of fishing mortality increased from 0.0 to 0.6 over a 25-yr period, the estimated stock numbers cycled down. Reducing fishing mortality over the next 50 yr from 0.6 to 0.4 curbed the downward trend in stock numbers and initiated fluctuations in the population with a peak-to-peak periodicity of 12 yr. Accompanying these fluctuations was a reduction in amplitude and a general increase in stock abundance.

Discussion

According to Brody (1945), egg production is related exponentially to food consumption. Wigley (1965) confirms that this relationship is well established among fish culturists. Grauman (1973) suggests that the condition of cod during egg development is an important factor influencing subsequent egg survival. However, Nikolsky (1965) states that stock fecundity decreased with food supply but there was no change in the amount of yolk associated with individual eggs. In accord, Tyler and Dunn (1975) found a positive and linear relationship between ration and ovary weight for winter flounder (*Pseudopleuronectes americanus*). A decline in ovary weight was due to a reduction in the number of yolk-bearing oocytes, this reduction being caused by a suppression of vitellogenesis and reabsorption of yolkless oocytes.

As the biomass of cod in the southern Gulf of St. Lawrence stock increases beyond 1.1×10^5 metric tons (Fig. 2), the average ration size presumably would be reduced. Tyler and Dunn's (1975) work would suggest that any decline in ration size would lead to a decline in the number of viable eggs per

female. At parent stock biomasses of 1.9×10^5 metric tons the catch of eggs is approaching zero; however, this does not mean that there are no eggs in the water column, but that the survey cruises were not intense enough to catch any eggs. Possibly, beyond stock biomasses of 1.9×10^5 metric tons, minimum egg survival is governed more by environmental factors than intrinsic density dependence.

At stock biomasses less than 1.1×10^5 metric tons, presumably spawning stock biomass becomes positively correlated with total fecundity. There are no data to show that the estimated spawning stock biomass has ever been this low and the implications from the curve should be treated with caution, although the relationship does have theoretical support. Unless the niche previously occupied by cod is filled by a competitor, most cod would be able to satiate and produce viable eggs.

As the temperature between years rises the number of eggs caught increases, due to improved survival. Hermamet al. (1965) found the highest correlations between temperature and year-class strength in May, during egg development and hatching, and July presumably being associated with larval survival. Forrester and Alderdice (1966) indicated the rate of development of Pacific and Atlantic cod eggs in relation to temperature was remarkably similar. Therefore, to conclude that both Atlantic and Pacific cod have an optimum temperature for the survival of eggs of near 7.1 C for salinities similar to the Gulf of St. Lawrence is quite valid. Holden (1970) found the temperatures in May below 8.58 C produced strong year-classes of cod in the North Sea. The greatest decline in temperature to 6.68 C produced one of the largest year-classes. Bonnet (1939) shows similar results: With a salinity of 32.31‰, egg survival was maximized at 6.5 C. Both the studies of Forrester and Alderdice (1966) and Bonnet (1939) indicate that the instantaneous mortality rate of eggs is greater at lower

than at higher temperatures. In accord, equation 1 indicates temperature is having an exponential effect when below optimum.

The effect of temperature on cod larvae is both direct, operating through bioenergetic responses and indirect, controlling the food supply. Changes in temperature have been shown to be important in determining variations of primary production in the Gulf (Steven 1974). Hjort (1914) postulated that mortality of larvae from starvation, due to an insufficient supply of plankton of suitable size, is the most important cause of the decline in abundance of a year-class. However, Grauman (1973) found the variation in food supply explained only 25% of the variation in larval abundance. A similar study by Corlett (1965) showed that the variations in abundance of plankton explained only 57.4% of the change in year-class strength of cod stocks in the western Barent Sea. The logarithmic nature of the relation indicated that increasing plankton densities had less effect on year-class strength. It would seem that when temperature is below that required to produce a threshold density (Kerr 1971) of plankton for larvae, small changes would be important in determining survival. However, when plankton reaches densities at which larvae can satiate, further rise in temperature, and the resulting increases in available food, would be of little importance.

Temperature affects the development rate of larvae and reduces the time spent drift feeding on slow-moving plankton (Sysoeva and Degtereva 1965). Since larvae at this stage are inefficient swimmers they are extremely susceptible to predation, as well as being reliant on temperature to determine their food supply. As they grow in length their ability to swim improves (Ryland 1963) so they are more able to avoid predators and gather food. Grauman (1973) can attribute 91% of the variation in cod larval length to varia-

tions in their food supply while Ponomarenko (1965) indicates that year-class strength was related to stomach fullness, fatness, and nutritional condition of cod fry. A rise in temperature is known to increase the appetite of fish (Brett 1971), and the basal metabolic rate (Saunders 1963; Beamish 1964; Beamish and Mookerjii 1964; Brett 1964), as well as the swimming speed at which fish can search for food (Rao 1968; Brett 1971). Using a system simulation, Lett and Beamish (unpublished data) have shown that the effect of temperature on appetite is one of the most important factors governing seasonal growth rates of fish.

The density-dependent relationship existing between larval abundance and juveniles 2 yr (Fig. 4) later does not begin until the cod fry become demersal since the relationship between cod eggs and larvae (Fig. 3) is linear showing no density dependence. There is some evidence that cod fry remain pelagic until they are 1⁺ (Halliday personal communication). In accord Ponomarenko (1973) established that year-class strength of cod is not determined in the first year of life. The major predators of 0⁺ group cod are usually older cod in the Barent Sea (Ponomarenko 1965), presumably a major population control factor. However, this may not be the case in the Gulf of St. Lawrence, but his observation that the high numbers of settling cod fry result in an increase in the number of predators able to live in the bottom layers would apply. Ponomarenko (1973) established that older cod usually never feed on fry after they have reached 10 cm in length. It follows that an alternate density-dependent mechanism must be operating simultaneously and this mechanism gains importance as cod grow. The 1⁺ cod at high densities could overcrop the available food supply. In the Gulf of St. Lawrence, small cod 11-20 cm feed primarily on a limited number of food forms consisting of mysids, euphausiids and amphipods (Powles 1958). The feedback time required for the populations of these

organisms to build back up would be relatively slow. Thus, an overcropping could lead to a reduction in nutritional status of young cod, again making them more susceptible to predation (Ponomarenko 1961).

The origin of the simulated fluctuations in stock numbers was explored using the simulation to conduct a controlled experiment. The two examples in Figure 6 are for a constant annual temperature cycle in the Gulf and fishing mortalities (F) of 0.4 and 0.6. The decline in stock biomass associated with fishing produced a rise in egg numbers (Fig. 2), and an increase in the number of larvae. This increment generated a peak abundance of juveniles, recruitable 4 yr later (Fig. 3, 4). The fluctuations are the result of a shift to the right across the density-dependent relationship between larvae and juveniles. Stock biomass continues to decline to a value that is on the left-hand limb of the egg production curve. When the first pulse of new recruits comes into the mature population, egg numbers go up, larval abundance increases and recruitment declines. However, three of the initially strong year-classes continue to dominate the spawning stock biomass producing three more poor year-classes, this effect diminishing each year. It follows that the entry of the small year-classes causes a resurgence of recruitment and subsequent parent stock biomass. A general pattern emerges; 4 years of decline in stock biomass from a previous peak generate 2 more years of decline and 2 years' recovery (a trough) which in turn leads to an additional 4 years of recovery. The periodicity for cod then is three times the average age at first maturity.

The long-term average stock size remained relatively uniform at both levels of exploitation, although the amplitude of the fluctuations was greater at $F = 0.6$. The recruitment mechanism responds, at the expense of population stability, by producing larger year-classes through the

density-dependent larvae juvenile relationship. However, when larvae abundance becomes so low that juvenile abundance is determined on the left-hand limb of the curve, the population cannot recover. That collapsing fish stocks tend to produce extremely strong year-classes, prior to a recruitment failure (Marr 1960; Regier 1973) is a common legacy. When the stock biomass occupies the left-hand limb of the egg production curve, cool spring and summer temperatures are indeed important since they could further reduce larval abundance through the density-dependent larval juvenile relationship, leading to a year-class failure.

It can be concluded from this study that temperature is exerting considerable influence on the quantity and stability of cod production, through the recruitment mechanism. Furthermore, it is interesting that cod catches/unit area increase moving south from Greenland, reaching a maximum in the southern Labrador-Newfoundland area, and then decline to a minimum near the southern range of the species on Georges Bank (D.M. Ware, personal communication). Although cod growth would change with temperature, the effect of temperature on the stock recruitment mechanism may be a more important factor governing cod production over the wide geographical area of the North Atlantic.

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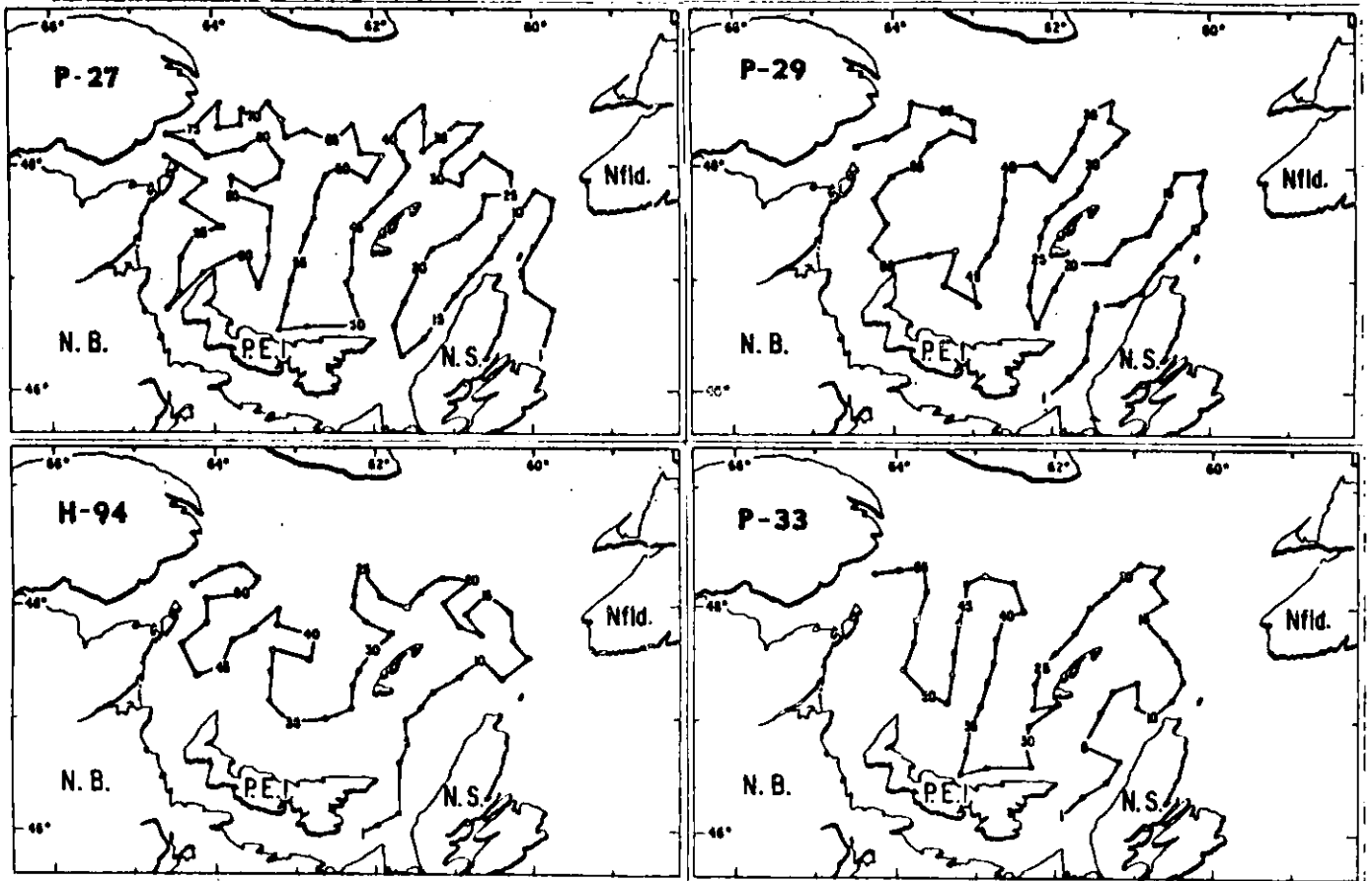


Fig. 1. Cruise tracks for egg and larval surveys in the Gulf of St. Lawrence for 1968. The times of the cruises were as follows: P027 23 May-4 June; P029 18-25 June; H094 25 July-5 August, and P033 17-31 August.

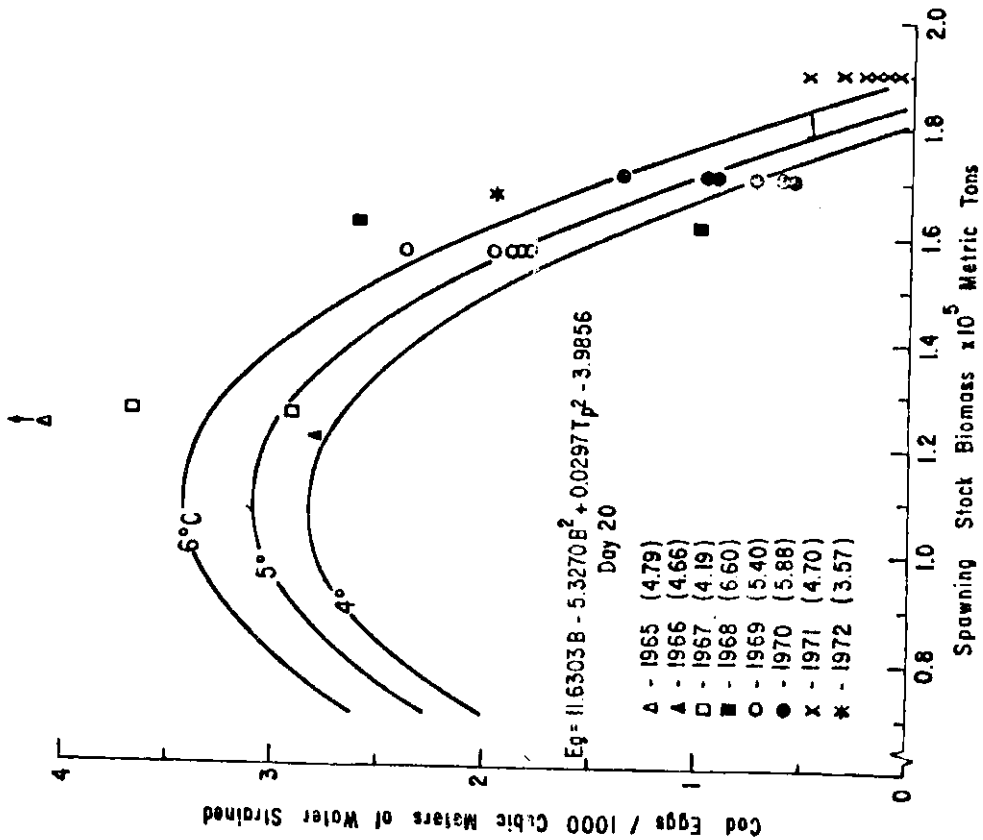


Fig. 2. Effect of estimated spawning stock biomass and temperature on the catch of cod eggs/1000 cu m of water strained. Points on the graph have been adjusted to estimate the abundance level on 20 May. Multiple points within years represent different depths which were treated as an estimate of pure error. The numbers in brackets are unadjusted surface temperatures.

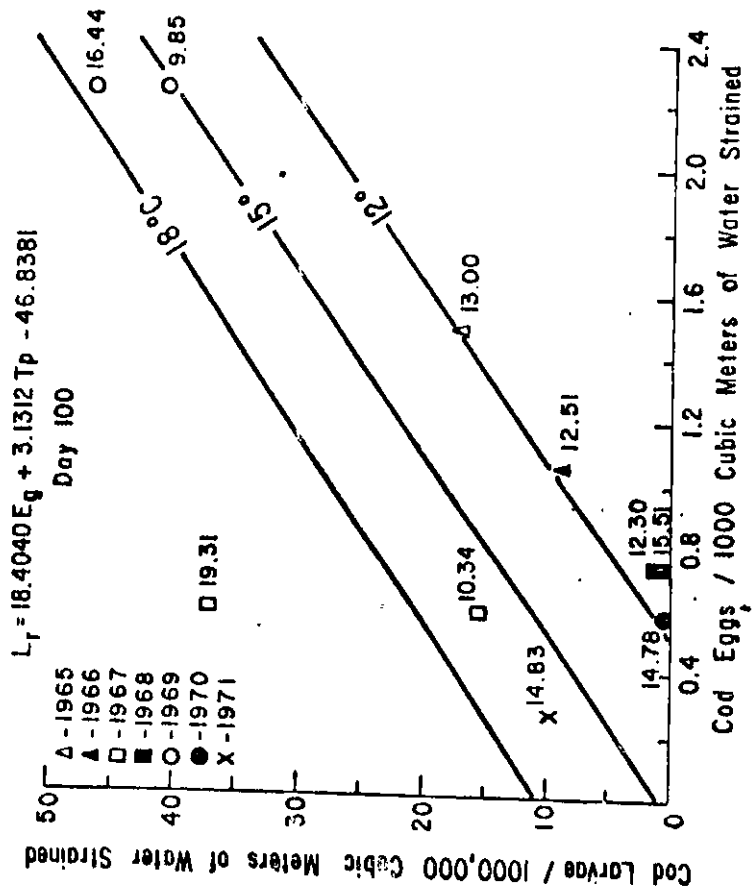


Fig. 3. Effect of catch of cod eggs/1000 cu m of water strained and temperature of the catch of cod larvae/100,000 cu m of water strained 100 days after 1 May. Data are unadjusted and numbers beside the points are sea surface temperatures.

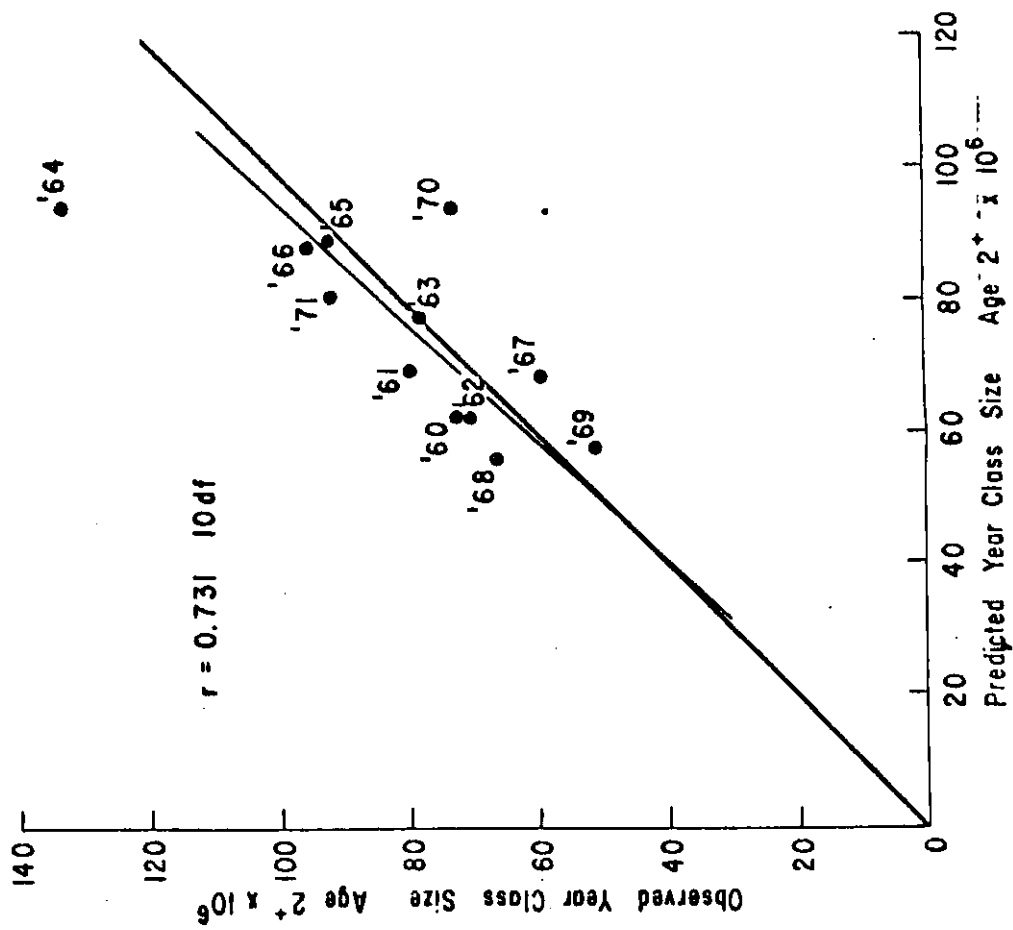


Fig. 5. The correlation between the simulated year-class size (predicted) and that estimated from juvenile surveys in the Gulf of St. Lawrence (observed). The line at 45° indicates parity between the two variables.

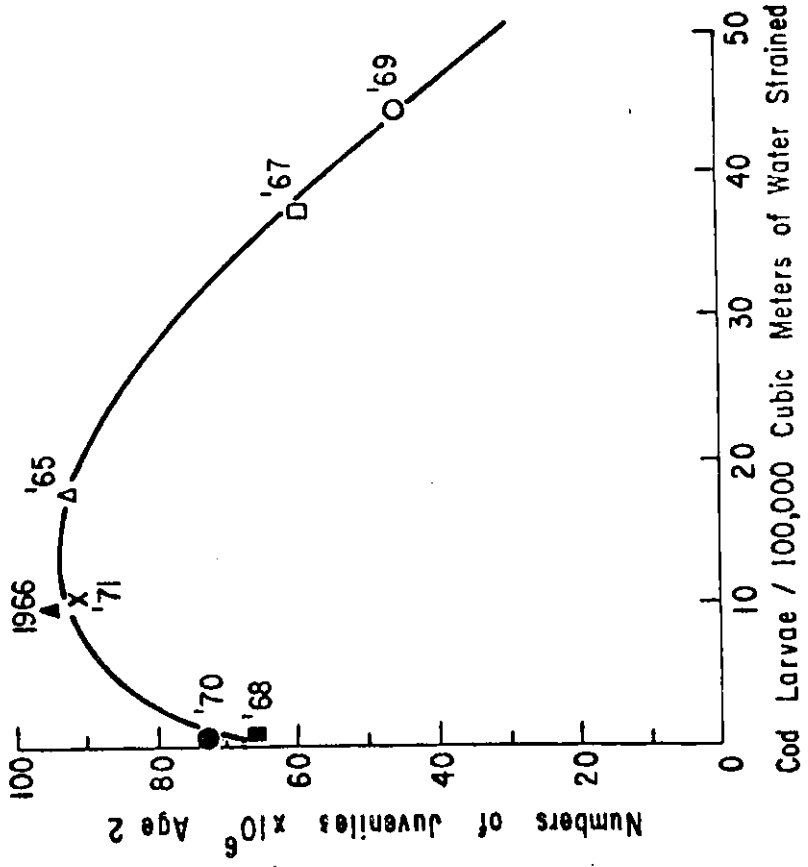


Fig. 4. Density-dependent relationship between the catch of cod larvae/100,000 cu m of water strained and the estimated number of 2+ cod from juvenile surveys.

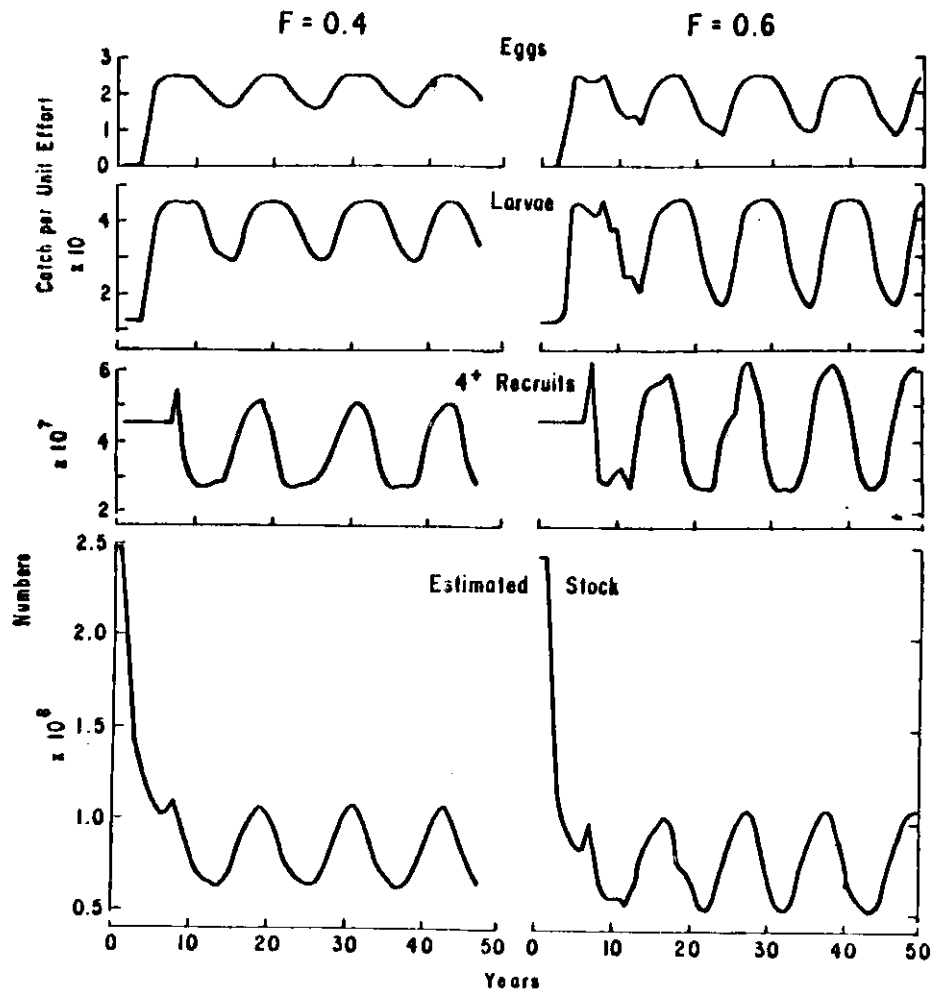


Fig. 6. Simulated effects of two levels of fishing mortality (0.4 and 0.6). Moving from the top of the page down, are abundance levels of eggs, larvae, 4+ recruits and adults are simulated over time.

Appendix 1. The frequency and dates of egg and larval cruises in the southern Gulf of St. Lawrence.

<u>Year</u>	<u>Number of cruises</u>	<u>Dates</u>
1965	3	May 27-June 6; Sept. 9-27; Sept. 28-30
1966	4	May 26-30; June 20-27; July 20-26; Sept. 13-22
1967	5	May 25-June 7; June 16-20; July 20-28; Aug. 22-31; Oct. 2-8
1968	4	May 23-June 3; June 18-25; July 25-Aug. 5; Aug. 17-31
1969	5	May 12-25; June 11-19; July 17-29; Aug. 19-30; Sept. 12-18
1970	2	May 20-28; Aug. 20-29;
1971	2	May 10-20; Aug. 24-Sept. 3
1972	1	May 16-31

Appendix 2. Grande-Rivière sea surface temperatures, estimated age 2⁺ juveniles corresponding to the adjacent temperature and spawning stock biomass data, and estimated spawning stock biomass for each year.

Year	Temperature at Grande-Rivière			Estimated year-class size at	Estimated spawning stock
	May 20	May 30	Temp. max.	age 2 ⁺ from juvenile surveys	biomass May 1st metric ton
1960	5.4 C	7.5 C	13.0 C	71,920,000	272,707
1961	4.5	6.0	13.7	79,858,000	292,342
1962	4.6	6.5	13.2	71,552,000	285,927
1963	4.7	7.1	14.2	78,012,000	216,567
1964	4.1	5.8	12.8	133,752,000	174,942
1965	4.4	6.0	13.0	92,039,000	122,631
1966	4.0	6.1	13.1	95,362,000	122,070
1967	3.9	6.2	16.5	59,371,000	124,886
1968	7.2	8.6	14.6	66,385,000	162,331
1969	5.2	6.7	13.6	45,713,000	157,379
1970	5.9	7.3	16.0	73,029,000	171,281
1971	5.8	7.3	14.4	91,855,000	189,997