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A system simulation to determine the implications of fluctuations in recruitment on management policies of fish stocks with special reference to Gulf of St. Lawrence cod

by

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INTRODUCTION

Historically, fisheries biologists, guided by such forerunners as Parrish and Jones (1953) and Ricker (1958) have rigorously studied the response of fish populations to exploitation, assuming constant recruitment independent of environmental effects. 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.

The Atlantic cod (*Gadus morhua* L.) stock under investigation, delineated by three tagging studies, has been shown to occupy only ICNAF Divisions 4T and 4Vn (McCracken 1959; Martin and Jean 1964; Kohler 1975). During the fall, cod 4<sup>+</sup> and older emigrate from the southern Gulf and overwinter on the edge of the Laurentian Channel east of Cape Breton. In May, they again migrate to spawn in the highly productive shallows of the southern Gulf (Paloheimo and Kohler 1968). This stock supports two fisheries, a winter component off Cape Breton, and a summer component in the southern Gulf of St. Lawrence. Increases in fishing effort are usually reflected in catches from the winter fishery, while fishing effort has remained relatively constant in the summer in the southern Gulf of St. Lawrence.

It is the aim of this paper to analyze the effect of temperature, as the key environmental factor, with parent stock biomass as the forcing functions of the stock recruitment mechanism for cod. The implications of these fluctuations in recruitment will be examined in relation to fisheries management strategy. The different management policies to be examined are the control of fishing effort, spawning stock biomass and catch.

#### METHODS

Data collections and amalgamation are discussed in Lett et al. (1975a). This data was analyzed by response surface techniques (Cochran and Cox 1968) to determine the relationship among the dependent and independent variables. The fitting procedure employed either a linear polynomial

$$Y = b_0X_0 + b_1X_1 + b_2X_2 + b_{11}X_1^2 + b_{22}X_2^2 + b_{12}X_1X_2$$

or the corresponding intrinsically linear model. The whole model was fitted using stepwise regression (Draper and Smith 1966) and the equation was accepted based on the minimization of the error mean square.

#### Derivation of equations

Sea surface temperature and estimated parent stock size were found to be major factors affecting the catch of cod eggs by survey during May (Fig. 1). The general relationships among these variables were described by the following intrinsically linear model:

$$(1) \sqrt{\log(Eg+1)} = 3.876B - 1.7033B^2 + 0.7444T_p - 0.0595T_p^2 - 3.4005$$

Variable	Coeff.	SE	Partial Corr. Coeff.
B	3.8786	0.6966	0.9411
B <sup>2</sup>	-1.7033	0.2888	-0.9470
T <sub>p</sub>	0.7444	0.4344	0.6506
T <sub>p</sub> <sup>2</sup>	-0.0595	0.0385	-0.7118

The coefficient of multiple determination ( $R^2$ ) was 0.930 while F for regression was  $13.3^1$  ( $F'_{4,4}/6.4$ ). The addition of  $T_p^2$  resulted in neither  $T_p$  nor  $T_p^2$  being significant alone; however, there was a substantial drop in the error mean square and a 5% rise in the coefficient of multiple determination. Thus, the second order effect can be considered a significant variable (Draper and Smith 1966). The correlation matrix of the intrinsically linear model are presented in Appendix I. Eg is the catch of eggs/1000 m<sup>3</sup> of water strained and B is the estimated stock biomass ( $\times 10^{-5}$ ) on May 1 for individuals 4 years and older (Appendix IV(A)), which is considered the age at first maturity (Powles 1958). Cohort analysis (Pope 1972) was used to estimate the numbers of cod present in the parent population on January 1.

The number of fish caught between January and May in ICNAF subdivisions 4T and 4Vn and the number lost to natural mortality ( $M = 0.2$ ) (Clayden 1972; Halliday 1972) were subtracted from the January 1 estimate to give the size of the spawning population. Mean weights for each age were determined from commercial sampling and multiplied by the numbers to give the parent stock biomass.

The abundance of eggs was found to decrease in relation to the second order effect of time (Lett et al. 1975a) and a correction was made using the linear model:

$$(2) \quad \text{Eg} = 11.6303\text{B} - 5.3270\text{B}^2 + 0.0297\text{T}_p^2 - 0.0039\text{T}_m^2 - 2.4256$$

Time  $T_m$  was the number of days to the midpoint of a cruise since May 1. For comparison, the egg abundance levels were all corrected to May 20 facilitating the elucidation of the true partial correlations of temperature and biomass. Peak spawning of cod is thought to occur between 3-5°C (Hjort 1919; Bigelow and Schroeder 1953) and the initiation of spawning was assumed to vary little from year to year in accord with Cushing's (1969) hypothesis. Spring bottom temperatures in the Gulf of St. Lawrence have remained remarkably uniform; therefore, May 20 represents some point on the egg production cycle which varies little annually, and represents the abundance of Stage II eggs.

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<sup>1</sup>Significant  $P < 0.05$ .

The sea surface temperatures taken on egg and larval cruises were well correlated with those at Grande Rivière ( $r = 0.77$ ) on the western shore of the southern Gulf of St. Lawrence.  $T_p$  then, is the mean sea surface temperature at Grande Rivière on May 20 (Lauzier 1969). These temperatures were used to avoid the variance problems associated with predicting cruise temperatures using the annual Grande Rivière cycle.

The quadratic nature of parent stock biomass (equation 1) suggests a density-dependent mechanism is controlling the number of eggs (Fig. 1). The general trend over the data series is a decline in egg numbers with increasing stock biomass; however, in 1973 stock biomass was so low that a reciprocal response was observed. 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 (Lett et al. 1975a).

The effect of temperature is also quadratic, although the  $\beta$ -coefficients indicate that only 32% of the total explained variation is attributable to temperature. The survival of cod eggs can be fitted to an optimum temperature of  $6.25^\circ\text{C}$  ( $\partial\sqrt{\log(\text{Eg}+1)}/\partial T_p = 0$ ) in accord with the findings of Forrester and Alderdice (1966) and Bonnet (1939).

The abundance of cod larvae  $L_R$  was found to be positively correlated with the catches of cod eggs (Eg) on May 20 but negatively correlated with time ( $T_m$ ) (Fig. 2a). The following intrinsically linear model, forced through the origin, described the relationship among the dependent and independent variables. The correlation matrix of the whole model is in Appendix II.

$$(3) \quad \log(L_R+1) = 3.1527 \log T_p \times \log(\text{Eg}+1) - 0.9709 \log T_m \\ \times \log(\text{Eg}+1) + 0.0221$$

Variable	Coeff.	SE	Partial Corr. Coeff.
$\log T_p \times \log(\text{Eg}+1)$	3.1527	1.7741	0.4420
$\log T_m \times \log(\text{Eg}+1)$	-0.9709	1.0024	-0.2594

The coefficient of multiple determination ( $R^2$ ) is 0.76 while  $F$  for regression is  $12.31^1$  ( $F'_{2,8}/4.5$ ) where  $L_R$  is the catch of larvae/100,000 m<sup>3</sup> of water strained,  $Eg$  is the catch of eggs adjusted to May 20/1000 m<sup>3</sup> of water strained and  $T_p$  is the annual mean monthly maximum sea temperature at Grande Rivière. The effect of the time x egg interaction is rather inconclusive, suggesting that the loss rate (Fig. 2a) is not profound for cod larvae in relation to the accuracy of abundance measurements over the time series analyzed. Density-dependent mortality at the larval stage is of marginal importance in determining the final number at metamorphosis, which is in accord with Hempel's (1965) hypothesis and our own findings for Atlantic herring (*Clupea harengus*) but in sharp contrast with our findings for Atlantic mackerel (*Scomber scombrus*) (Lett et al. 1975b). As the temperature increased the survival of cod larvae increases exponentially as found by Hermann et al. (1965) for cod larvae at West Greenland.

Equations (1) and (3) were used to predict the numbers of larvae on July 20 for the particular stock biomasses and temperatures which existed in the years 1963-1970. These larval abundance levels were then compared with the year-class sizes from cohort analysis and stock biomasses 2 years later using the following intrinsically linear multivariate relationship. The equation was forced to approach zero when there were no larvae. The correlation matrix is in Appendix III.

$$(4) \quad \log \frac{Y_{\max} - Y_R}{Y_R} = -6.1121 \log L_R + 1.1675 [\log L_R]^2 + 0.7131B \times L_R + 2.9320$$

Variable	Coeff.	SE	Partial Corr. Coeff.
$\log L_R$	-6.1121	1.0710	-0.8959
$[\log L_R]^2$	1.1675	0.2497	0.8555
$B \times \log L_R$	0.7131	0.2929	0.6523

The coefficient of multiple determination ( $R^2$ ) is 0.87 while  $F$  for regression is  $11.32^1$  ( $F'_{3,5}/5.4$ ) where  $Y_{\max}$  (130,000) is the maximum year-class strength observed since 1960 and is assumed to represent an asymptotic year-class strength as long as the total pelagic biomass (herring and mackerel) remains relatively constant.

However, B in equation 4 represents the biomass of adult cod 4 years and older. The relationship of adult cod biomass and year-class strength is sigmoid and negatively correlated (Fig. 3) as a result of the younger cod having to fit into a productive constraint on the adult cod biomass. The dependence of year-class strength on the number of larvae ( $L_R$ ) is log normal with the ascending limb of the curve being density dependent i.e., (cannibalism (Ricker 1954)) as well as the descending limb. This effect demonstrated by the  $L_R \times B$  interaction. Equation (4) can be transformed to a non-linear form.

$$(5) \quad Y_R = Y_{\max} / \text{ANTILOG}(-6.112 \log L_R + 1.675(\log L_R)^2 + 0.713B \\ \times \log L_R + 2.934) + 1$$

#### Model structure

A system simulation (Fig. 4) was constructed combining the structural equations relating biomass to growth and numbers of 2+ recruits and biomass and temperature to egg and larval numbers with an estimated selection ogive for 4 1/2-inch mesh otter trawl nets to allow the long-term effects of various management strategies on the southern Gulf of St. Lawrence cod stock to be examined.

The simulation was initialized by entering numbers at age  $N_a$  and mean weights at age  $W_a$  for ages 3-16 and selecting a level of fishing mortality for the summer fishery and a level of fishing mortality or a spawning stock biomass or a catch quota for the winter fishery.

After initialization, the population biomass for ages 4-16 was calculated by the formula

$$B_{TOT} = \sum N_a W_a \times 10^{-8}.$$

This biomass determines the pre-winter growth rate for ages 3-16 and, together with larval numbers, the number of age 2+ recruits.

The growth equation used is

$$(6) \quad W_a \text{ Exp}[0.5(0.55/(1 + \text{Exp}(0.6B_{TOT} - 1)))] + W_a$$

Growth occurs twice annually in the model, before the summer and winter fisheries.

If the option of catch quota control or spawning stock biomass control was selected, then a level of F was estimated immediately prior to the winter fishery so that the desired catch or stock biomass subsequent to the winter fishery was obtained. Due to computing speed limitations of the machine used to implement the model, an approximation ignoring the shift in selection at age due to changes in growth rate was employed so that catch or biomass was controlled within narrow limits. Under biomass regulation, if the stock biomass before the winter fishery was less than the required level, F was set to zero.

Selections at age factors  $\partial_a$  were calculated for each fishery by transforming mean weight at age  $W_a$  to length at age  $L_a$  using a weight-length key

$$(7) \quad L_a \text{ (cm)} = 10 \uparrow ((\text{Log } W_a + 5.16)/3.05)$$

( $10 \uparrow$  means 10 raised to the power), based on keys derived for southern Gulf of St. Lawrence cod by Kohler et al. (1970). The selection ogive was the cumulative distribution function of a normally distributed random variable with mean 40 cm and standard deviation 7.5 cm derived from data in Holden(ed) 1971.

$$(8) \quad \partial_a = \frac{1}{7.5\sqrt{2\pi}} \int_0^{L_a} \text{Exp} - ((x-40)/7.5)^2 dx$$

In both the summer and winter fisheries, the standard catch equation (Beverton and Holt 1957) with a semi-annual natural mortality of 0.1 was used.

$$(9) \quad Y = \frac{\sum N_a W_a \partial_a F (1 - \text{Exp}(-(\partial_a F + 0.1)))}{\partial_a F + M}$$

Following each fishery, the numbers at ages 3-16 were reduced by the catch at age and one half of the annual natural mortality by the relation

$$(10) \quad N_a \text{ Exp}(-(\theta_a F + 0.1)) \rightarrow N_a$$

The update of numbers at age and weight at age occurred after the winter fishery and immediately before the calculation of spawning stock biomass. A total mortality rate of 0.2 was applied to age 2+ recruits and a weight at age 2+ of 0.3 kg was assumed.

The spawning stock biomass (ages 4-16) was calculated as

$$(11) \quad B_{SS} = \sum N_a W_a \times 10^{-8}$$

Egg production was then calculated as  $C \cdot |C|$  where

$$(12) \quad C = \sqrt{\log(\text{Eg}+1)} = 3.87B_{SS} - 1.70B_{SS}^2 + 0.056T_p^2 - 3.4$$

where  $T_p$  was a random normal deviate with mean 5.01 and standard deviation 1.11, based on observed sea surface temperatures at Grande Rivière.  $\log(\text{Eg}+1)$  was constrained to be non negative.

The number of eggs was combined with a second random temperature deviate, independent of the first and normally distributed with mean 14.39 and standard deviation 1.28 derived from mean monthly maximum sea surface temperatures at Grande Rivière to calculate a number of larvae using the equation

$$(13) \quad \log(L_R+1) = 3.15 \log T_p \times \log(\text{Eg}+1) - 1.85 \log(\text{Eg}+1) \\ - 0.0221$$

Temperatures in May were uncorrelated with the monthly maximum usually occurring in August. Grande Rivière temperatures in May (Lauzier 1969) had a correlation of  $r = 0.79$  with those collected on plankton cruises. The number of larvae was used to determine the number of age 2+ fish two years later.

The number of age 2+ recruits was calculated using the population biomass  $B_{TOT}$  prior to the previous winter fishery and the number of larvae two years previous according to the relation



$$(14) \quad N_2 = X \times 130 \times 10^6 / [10 + (1.68(\log L_R)^2 - 6.11 \log L_R + 0.71 B_{TOT} \times \log L_R + 2.93) + 1]$$

X was a random variable whose natural logarithm was normally distributed with mean 0 and standard deviation 0.1. The random multiplier X was introduced in the calculation of age 2+ recruits because 13% of the observed variance in recruitment was unexplained by the regression equation and ignoring this residual variation results in spurious stability of recruitment at extreme levels of biomass.

Growth was applied to weight at age for ages 3-16 prior to the summer fishery using the same formula as before the winter fishery with  $B_{SS}$  substituted for  $B_{TOT}$ .

The summer fishery was carried out at a preset level of F. The mesh selection calculations and catch equation were the same as for the winter fishery.

Following the summer fishery, the numbers at age were reduced by the formula

$$(15) \quad N_a \text{ Exp}(-(\theta_a F + 0.1)) \cdot N_a$$

and the yearly cycle of events began again with the calculation of  $B_{TOT}$ .

In this model, each year is divided into two intervals corresponding to the two fisheries with a semi-annual mortality rate of 0.1 applied to each interval. Growth rates and, through them, selection at age factors respond on a semi-annual basis to changes in stock biomass.

#### The biological basis of the model

The abundance of cod eggs is directly related to the growth rate of the adult stock (Fig. 5) and may be still better explained by the production of the adult cod ( $P = B \frac{dw}{dt}$ ). It would seem that the growth rate then, is providing the homeostatic core of the recruitment mechanism. Furthermore, it can be hypothesized that growth rate is a determining variable controlling the entire dynamics of the cod population. The annual abundance of Stage I herring larvae is determined by herring production (Fig. 6) when environmental effects are removed.

These results are not surprising in light of the work by Scott (1962) and Tyler and Dunn (1975). They found that the fecundity of rainbow trout (*Salmo gairdneri*) and winter flounder (*Pseudopleuronectes americanus*) was positively and linearly related to ration size (Fig. 7a). A threefold decline in ovary weight in relation to a twofold reduction in ration was due to a decline in the number of yolk bearing oocytes (Fig. 7b), this decline caused by a suppression in vitellogenesis and reabsorption of yolkless oocytes (Tyler and Dunn 1975). Bagenal (1966) related changes in the fecundity of plaice to an increase in the availability of food due to a reduction in the population biomass. He went on to conclude the fecundity of the population is modified by food availability, and that fecundity acts as a density-dependent population regulatory mechanism. The same sort of density-dependent egg production mechanism has been noted for Atlantic mackerel (*Scomber scombrus*) (Lett et al. 1975b) and North Sea plaice (*Pleuronectes platessa* L.) (P. F. Lett, D. Harding, and R. C. A. Bannister, unpublished data). The second order relationship between egg production and stock biomass (Fig. 1) is only feasible when there is also density-dependent growth. For Gulf of St. Lawrence cod stock, the relationship between parent stock biomass and the instantaneous growth rate is clearly demonstrated (Fig. 8). For North Sea plaice, this relationship is not as lucid; however, it does exist (Bannister 1975), which disagrees with Cushing's (1975) hypothesis and the basic premise of the Beverton and Holt (1957) yield per recruit model. Using multivariate techniques no changes in the growth rate of Gulf of St. Lawrence Atlantic herring 2+ and older could be attributed to changes in the biomass. The factors found to explain 89% of the changes in growth rate were temperature, the abundance of juvenile mackerel and the interaction of age x temperature. This outcome suggests a basic difference between the recruitment mechanisms of herring and the two demersal species. However, in both cod and herring egg production is closely linked to the growth rate.

The number of cod eggs caught on research cruises increases with temperature due to improved survival. Forrester and Alderdice (1966) indicated that both Atlantic and Pacific cod have an optimum temperature for the survival of eggs near 7.1°C for salinities similar to those observed in the Gulf of St. Lawrence. Bonnet (1939) shows similar results: with salinity of 32.31‰ egg production is maximized at 6.5°C.

As the number of cod eggs increases, the number of larvae also increases; furthermore, this increase is exponential (Fig. 2). The suggestion is that faster growing, better conditioned fish will produce more eggs (Fig. 5 and 6) and also more viable eggs (Fig. 7b) (Nikolsky 1969; Tyler and Dunn 1975).

The survival of cod larvae seems to be weakly density-dependent (Fig. 2b) with the final number being almost constant no matter what the initial number. However, metamorphosis would occur before this limiting value could be reached. In contrast, the density-dependence in the larval stages of Atlantic mackerel is extremely strong (Lett et al. 1975b) suggesting a basic difference in the recruitment mechanisms of the two species. Possibly this is related to mackerel being pelagic feeders able to prey on their own larvae, while cod are semi pelagic or demersal, not able to feed on juveniles until they become demersal. In addition, mackerel larvae are cannibalistic, the larger larvae feeding on the smaller ones (Arnold 1970), while the death of cod larvae is a function of the competition, starvation sequence (Ware 1975).

The effect of temperature on cod larvae is greater than pure density-dependence in determining the final number at metamorphosis, and this effect increases exponentially (Fig. 2a) (Bannister et al. 1974). Temperature acts both directly operating through bioenergetic responses and indirectly by controlling the food supply. Changes in temperature have been shown to be important in determining variations in primary production in the Gulf (Steven 1974; Denman and Platt 1975). Hjort (1914) and Jones (1973) postulate that mortality of larvae from starvation due to an insufficient supply of plankton of suitable size is the most important cause of a decline in abundance of a year-class. It follows that temperature mediated through the density-dependent process also could lead to a substantial mortality. However, Grauman (1973) found the variations in food supply explained only 25% of the variations in larval abundance in the Barent Sea. A similar study by Corlett (1965) showed that the variations in abundance of plankton explained 57.4% of the changes in year-class strength of cod stock in the western Barent Sea. The logarithmic nature of the relation indicated that increasing plankton densities have proportionally 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 rises 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 drift feeding on slow moving plankton (Sysoeva and Degtereva 1965). Since fish living at lower temperatures have evolved to spawn larger eggs (Ware 1975) with larger yolk sacs associated with the larvae (Blaxter and Hempel 1963), to survive this period, it would tend to suggest that this is an important period in the early life history of the fish. Larvae at this stage are inefficient swimmers and 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 better able to avoid predators and gather food. Grauman (1973) can attribute 91% of the variations in cod larvae length to variations in their food supply. 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, P. F. Lett and F. W. H. Beamish (unpublished data) have shown the effect of temperature on appetite as one of the most important factors governing seasonal growth rates of fish.

The final density-dependent relationship, and probably the most important step in the recruitment mechanism existing between larval abundance and juveniles 2 years later (Fig. 3), does not begin until the cod fry become semi-pelagic or demersal, since density dependence in the larval stage is weak. There is some evidence that cod fry remain pelagic until they are 1+ (R. G. Halliday, personal communication). The results of juvenile surveys indicate the number of 1+ cod associated in catches with 2+ and 3+ is low (A. C. Kohler, unpublished data). In accord, Ponomarenko (1973) established the year-class strength of cod is not determined in the first year of life.

The simulated biomass was found to be sensitive to the size of cod juveniles at the end of their second year of life. This parameter was held constant at 0.30 kg which was a long term average value. However, it was quite clear that maintaining a uniform size for cod upon entry into their demersal phase could be an important population stabilizing mechanism. The full explanation of this mechanism is dependent on the back calculation cod growth which to date is not complete.

The  $l_1$  size is an important link in the recruitment mechanism of the California sardine (Iles 1973) (Fig. 9). This same mechanism can be demonstrated for Gulf of St. Lawrence herring which show a clear relationship between year-class size and  $l_1$  length (P. F. Lett and A. C. Kohler, unpublished data). However, as previously stated, no density-dependent growth process has been demonstrated following the first year of life; therefore, the regulation of stock biomass must take place within the first year.

A constant annual growth rate will occur for fish over 1+ if the environment is stable (i.e., temperature and juvenile mackerel abundance). If maturity is a constant function of length, the size of the fish at the end of its first year of life would determine when it would mature (Burd and Cushing 1962), thus the amount of gonadal product elaborated by the parent stock would depend only on the number of mature individuals. In this way, a wave of large year-classes would produce a wave of small year-classes much in the way described by Jones and Hall (1974). However, the smallest perturbation would cause this system to become unstable. Therefore, for a fish species which only experiences density-dependent growth in the first year of life there must be an alternative stabilizing mechanism.

This mechanism is more clearly elucidated by considering Fig. 9. The mean abundance of  $l_1$  sardines falls directly below the peak of the annual production curve, not the biomass curve as postulated by Iles (1973). If the sardine is indeed maximizing its production in the first year of life, it would imply a mechanism whereby the year-class could simultaneously tend toward a constant mean  $l_1$  as well as constant numbers, thereby offsetting the destabilizing forces of a random environment. The method by which both sardines and herring do this is a density-dependent process in which the individual competes with the remaining cohort biomass, such that growth rate and mortality are inversely related (Cushing 1975; Ware 1975). If the carrying capacity of the 0-group herring and sardines is fixed, there is some optimal trade-off between fish size and biomass which can utilize the available production in an optimal way. This optimum is achieved by the juvenile cohort converging into the balance point between individual weight and cohort biomass where

$$(16) \quad - \frac{dw}{w} = \frac{dB}{B}$$

Dividing through by dt gives

$$(17) \quad - \frac{dw}{dt} \cdot \frac{1}{w} = \frac{dB}{dt} \cdot \frac{1}{B}$$

Since the instantaneous growth rate of the individual is

$$(18) \quad G = \frac{dw}{dt} \cdot \frac{1}{w}$$

expression (3) is equal to the instantaneous growth rate of the cohort.

$$(19) \quad -G = \frac{dB}{dt} \cdot \frac{1}{B}$$

The turnover rate or the ratio of production to biomass

$$(20) \quad P/B = \frac{dB}{dt} \cdot \frac{1}{B} \quad \text{Dickie (1972).}$$

has been defined by Baranov (1918) to be

$$(21) \quad P/B = (F + M)$$

where F is the level of fishing mortality and M is the level of natural mortality. Therefore, this balance point toward which the year-class converges is defined by

$$(22) \quad G = -M$$

since fishing mortality is zero on the 0-group fish. Therefore, maximum production is achieved when the instantaneous growth rate balances the mortality rate. This point optimizes both year-class size and growth simultaneously in addition to supplying a population stabilizing mechanism. Variations from the convergence to maximum production by the juvenile cohort are the result of divergence from the optimal feedback time between biomass and growth rate for a given level of the environment. These deviations in feedback time are linked to disruptions in the foraging efficiency of the animal due to environmental heterogeneity and subtle bioenergetic changes.

This mechanism may only be true for fish stocks which exhibit no cannibalism, only competition. The major predator of 0+, 1+ and 2+ cod is usually older cod (Bigelow and Schroeder 1953; Ponomarenko 1965), presumably a major population control factor. Ponomarenko (1973) established the older cod usually do not feed on juveniles after they reach 10 cm in length; however, Bigelow and Schroeder (1953) state the adult cod feed on their juveniles until they are over 20 cm in length. Therefore, an alternative density-dependent mechanism must be operating, and this mechanism gains in importance as the cod grow. The 1+ and 2+ cod at high densities could overcrop the available food supply. In the Gulf small cod, 11-20 cm, feed primarily on a limited number of food forms consisting of mysids, euphausiids and amphipods (Powles 1958). The turnover time required for the populations of these organisms to build up again after depletion would be relatively long. Thus, overcropping could lead to a reduction in nutritional status of young cod, again making them more susceptible to predation (Ponomarenko 1961).

The entire cod production system is constrained by the pelagic fish biomass and the model of this paper represents the fishery when it is operating within the constraint of constant total pelagic biomass. During 1955-59, year-class strengths of cod were well correlated with a severely reduced total pelagic biomass brought about by the epizootic disease in the Gulf of St. Lawrence (Sinderman 1958). At this time, year-class strengths were excessive with the 1956 year-class being twice as large as any observed before or after this epidemic. This is explained by the carrying capacity for young cod being substantially improved, since the energy harvested by pelagic fish species could now be transferred into food organisms eaten by juvenile cod. The growth rate of adult cod also improved (Kohler 1964) due to increased availability of food, which may have substantially incremented the production of eggs for a given population number. The homeostatic mechanisms regulating the abundance of cod must fit within the carrying capacity left vacant by pelagic species. As the population is being reduced by exploitation, the surplus energy is simultaneously being synthesized into both somatic and gonad growth. Thus, the attainment of maximum growth rate is the lowest level of population biomass at which the stock can replace itself on an annual basis.

#### Simulation results

Three types of management strategy were considered, fixed catch quota, fixed fishing mortality (effort quota) and maintenance of a fixed spawning stock biomass.

In the absence of fishing, the simulated stock size exhibited a cyclic behaviour, rising from  $50-60 \times 10^3$  m.t. to  $250-300 \times 10^3$  m.t. in 6-8 years, declining slowly for 6-8 years and declining sharply to  $50-60 \times 10^3$  m.t. in 6 years. About 15 years were required for one cycle.

The introduction of a catch quota of  $10-15 \times 10^3$  m.t. in the winter fishery reduced the peak biomass, but the cyclic behaviour was qualitatively unchanged. The associated levels of fishing mortality varied from 0.04 to 0.4. Increasing the quota to  $20-25 \times 10^3$  m.t. did not remove the 16-year cycles in biomass and effort. When the quota was raised to approximately  $30 \times 10^3$  m.t., the stock declined to zero after five cycles. Changes in the quota level had little effect on the amplitude of the natural cyclic trend (Fig. 10) in biomass and led to high levels of fishing mortality at low population biomasses.

The effects of equal, constant fishing mortality rates for the summer and winter fisheries is illustrated in Fig. 11. Simulations were run for 50-100 years to ensure that the effects of the initial conditions were removed. Mean

catches and standard deviations were calculated from a 10-year series after simulation had stabilized. A fishing mortality rate of  $F = 0.2$  resulted in irregular fluctuations in biomass between  $100-200 \times 10^3$  m.t. with catches averaging  $31 \times 10^3$  m.t. with a standard deviation (SD) of  $2.9 \times 10^3$  m.t. Increasing  $F$  to  $0.4$  reduced the range of fluctuations to  $65-175 \times 10^3$  m.t. with mean catch of  $42 \times 10^3$  m.t. and SD of  $2.2 \times 10^3$  m.t. When  $F$  was  $0.7$ , the spawning stock biomass stabilized at  $85 \times 10^3$  m.t. with a catch of  $53 \times 10^3$  m.t. and SD of  $0.25$  m.t. Increasing  $F$  to  $0.9$  caused the stock biomass to become unstable and decline to zero. Fig. 13a shows the relationship between fishing effort and yield and Fig. 14 shows the relationship between fishing effort and SD of catch. The scatter of points in Fig. 13a is due to the inclusion of simulations with unequal allocation of effort to the two fisheries.

In order to study the effects of differing allocations of effort to the two fisheries, simulations were carried out with the total fishing mortality rate in the range  $0.3-0.6$ . The results are given below:

F Summer	F Winter	Total yield (m.t. $\times 10^{-3}$ )
0.1	0.2	37.1
0.2	0.1	42.4
0.15	0.3	40.9
0.3	0.15	47.6
0.25	0.25	48.2
0.2	0.4	50.3
0.3	0.3	49.8
0.4	0.2	51.8

In all cases, the yield was increased by allocating more fishing effort to the summer fishery than to the winter fishery.

The results of simulations involving biomass control are illustrated in Fig. 12 and 15. In these simulations, the summer fishing mortality rate was zero. The results are as follows:

Biomass ( $B_{SS}$ ) $\times 10^{-3}$ m.t.	50	92	120	150	170
Yield $\times 10^3$ m.t.	52.0	52.5	42.7	44.3	31.5
SD of yield $\times 10^{-3}$ m.t.	13.0	3.8	19.7	2.3	13.4

Recruitment fluctuations were smallest near  $90$  and  $150 \times 10^3$  m.t.



### Model limitations

In the study of a natural system as large as the cod stock of the southern Gulf of St. Lawrence, it is not possible to take observations of stock size, temperature and other variables at all the levels necessary to accurately define response surfaces over the whole range of stock sizes and environmental variation. One cannot recommend overfishing a stock in order to study its behaviour on the verge of collapse. While accepting this constraint and attempting to make the best use of the available data, the analyst should note the areas where response surfaces are poorly supported by the available data. With the exception of the 1973 value of  $63 \times 10^3$  m.t. in the egg production analysis, the stock biomasses used in the derivation of the model equations lay in the interval  $120-240 \times 10^3$  m.t. The model equations predict egg productions which approach zero and subsequent minimal recruitments for biomasses below  $40 \times 10^3$  m.t. and above  $200 \times 10^3$  m.t. While these predictions are qualitatively reasonable since, for example, there can be no egg production at zero biomass, the accuracy of quantitative predictions diminishes sharply with increased deviations from the mean of the observed biomasses.

Although, under favourable environmental conditions, numbers of larvae in excess of  $10^5/1000 \text{ m}^3$  are predicted, the maximum larval abundance used in fitting the equation predicting age 2+ recruits was  $2.5 \times 10^4/1000 \text{ m}^3$  so that predicted low recruitments due to excessive egg and larval numbers at stock biomasses near  $125 \times 10^3$  m.t. are unsupported by observation.

The implications of these limitations on the behaviour of the model are that recruitment predictions at very high and very low levels of stock biomass are quantitatively variable although qualitatively acceptable and that the predicted variability of recruitment at biomasses near  $125 \times 10^3$  m.t. may be exaggerated. Thus the quantitative simulation results for strategies involving excursions into regions of very high and very low biomass are not well supported. Fortunately, strategies involving such extreme biomasses are less promising than those with biomass variations between  $90$  and  $190 \times 10^3$  m.t., so that the practical management of the fishery is not affected. The asymptotic nature of the equation predicting age 2+ recruits may result in an unrealistic stabilization of recruitment for biomasses below  $100 \times 10^3$  m.t. so that yield at high levels of fishing mortality may be overestimated. The predicted fluctuations in recruitment near  $125 \times 10^3$  m.t. have some influence in depressing yield and substantial influence in increasing the variability of catch from year to year (Fig. 15).

A weight of 0.3 kg was assumed for age 2+ fish independently of events in the fishery. It is likely that this weight, in fact, varies with year-class size and stock biomass although no substantial evidence supporting this hypothesis is currently available. A possible biological mechanism whereby fish tend to stabilize  $l_1$  and  $l_2$  length is discussed in the following section. Quantitative results of simulations are sensitive to the weight of age 2+ fish with higher yields and excursions into regions of higher stock biomass when this weight is increased, although qualitative results are similar.

The model equations were derived with observations during a period when the pelagic (herring and mackerel) fish biomass was fairly constant. There is evidence that environmental carrying capacity for cod is inversely related to the pelagic fish biomass. If the herring and mackerel stocks in the Gulf of St. Lawrence were depleted, as happened in 1954 with an epidemic of the epizootic disease, cod growth rates would increase (Kohler 1964) and maximum egg production for cod would occur at a higher stock biomass. Thus, the simulation results are conditional on stability of the pelagic biomass.

#### DISCUSSION

Three methods of regulating the fishery have been considered (1) catch quota (2) effort and (3) biomass control. The strategy of constant catch quota does little to damp the 15-year cycle of the unfished stock (Fig. 10). The upshot of this strategy is large fluctuations in fishing mortality rates; these rates increasing as the stock declines. In essence, the control of catch tends to augment the natural cyclical nature of the fishery and leads to stock collapses at levels below what is considered to be the maximum sustainable yield (MSY). Depending on the management strategy the MSY is between  $40-50 \times 10^{-3}$  m.t. However, with an annual catch quota of only  $35 \times 10^{-3}$  m.t., the stock eventually collapses. While the length and amplitude of the simulated cycles depends on the age at first maturity and the population structure, the amplitude of the simulated fluctuations may differ somewhat from those of the actual stock. The maximum catch which can be taken each year is not well defined, but it is clear that quota management is the poorest of all three choices since it does nothing to stabilize the stock biomass at a productive level.

A steady increase in yield with a reduction in variance results from the control of fishing mortality (analogous to effort control) (Fig. 12). The natural cycles of the unfished stock are opposed by taking larger catches above the average biomass and smaller catches below it. Simulation studies indicate a stabilization of biomass at  $85 \times 10^3$  m.t. and a catch at  $53 \times 10^3$  m.t. when  $F = 0.6$ . When  $F$  increases

to 0.9, recruitment becomes unstable and the stock eventually crashes (Fig. 11). The stability in the stock is a result of the relationship between larvae and the abundance of 2+ recruits (Fig. 3). When the stock biomass is low the curve becomes flat topped so that wide variations in larval number due to environmental influences and near maximum egg production result in very little change in the recruitable year-class size. However, when the stock is maintained below  $100 \times 10^3$  m.t., the fishery is on the edge of the precipice (Fig. 13a) and relies on a succession of maximal recruitments. In view of the lack of supporting biomass observations below  $100 \times 10^3$  m.t., the precise location of this precipice cannot be determined from the current model and to adopt a level of  $F = 0.6$  risks a collapse of the fishery.

Simulation results indicate that more effort should be applied to the summer fishery than to the winter fishery. This strategy improves the average level of recruitment for a given total  $F$  by reducing  $B_{ss}$  and also has the benefit of allowing the winter fishery to be used to "trim" the parent stock biomass on the basis of results from the summer fishery. Since the fish are much more highly concentrated in the winter fishery, they are much more accessible to trawling. Over the years this has resulted in the stock being "fished-up" to the point that only one year-class is primarily responsible for production of eggs. These mainly 4+ and some 3+ cod are going to spawn for the first time in the following spring and must be allowed to do so in order to maintain the stock. Therefore, when stock biomass is low, comprised of mainly young fish, the fishery should be maintained at an extremely low level.

The strategy of controlling spawning stock biomass enables larger catches to be taken at lower levels of  $F$  than is possible by effort control although fluctuations in fishing mortality require the effort levels to fluctuate. Fluctuations in catch are comparable at low levels of  $F$  with somewhat smaller fluctuations using biomass control. Managing the stock biomass at  $90 \times 10^3$  m.t. gives a slightly higher yield and variance in yield than setting  $F$  at 0.6. Because of the nearby constant recruitment at this stock size, the two strategies are almost equivalent. Regulating biomass is possible at  $50 \times 10^3$  m.t. at the cost of large fluctuations in catch and effort; this is not possible with a fixed effort quota. The striking decline in yield and increase in variance resulting from fixing the biomass at  $120 \times 10^3$  m.t. (Fig. 15) is a result of being on the peak of the egg production curve. Large numbers of larvae are being produced at this level of egg production. Due to the effect of biomass in reducing the number of recruits when larvae are abundant, the result is considerable fluctuations in recruitment and hence in catch with a slight loss in yield. The extreme stability of catch at  $150 \times 10^3$  m.t. is due in part to the location of the biomass half way down the right limb of the egg production

curve which would assure stable recruitment (Fig. 2). In addition, biomass is located near the point of inflection of the growth rate relationship so that small deviations in biomass are quickly compensated for by instantaneous increases in growth, thus maintaining biomass naturally at a constant level. As well as being able to respond to fluctuations in fishing intensity within a year, it can also equilibrate quickly to fluctuations in recruitment.

The importance of random fluctuations in determining the relation of yield to fishing mortality is evident in the comparison of Fig. 13a, b and c. Fluctuations in recruitment reduce the yield at low levels of  $F$  shortening the plateau near constant yield in Fig. 13c. The comparison of the yield vs fishing mortality curves for cod and mackerel (Fig. 13b) indicates a similar relationship between the two species with the production of mackerel being 10 times greater. This observation is not without ecological significance since mackerel occupy a trophic status one level below cod. The variance in catch was found to change considerably with changes with the levels of fishing mortality or biomass control. The failure of management by constant catch quotas was mainly due to cyclic trends in stock size and recruitment although random variations in recruitment was responsible for the collapse of the fishery at high quota levels.

The two components of variations in recruitment consisting of cyclic trends induced by the lag time between egg production and recruitment and random, environmentally induced, fluctuations in recruitment are the causes of the differing behaviour of the simulations under different management policies with the same average yield. In order to obtain consistently high catches with a resulting high average catch or yield, it is essential to stabilize the stock biomass in a productive region. In this model there are two stable productive regions, one near  $90 \times 10^3$  m.t. when stability arises through constant recruitment and the other near  $150 \times 10^3$  m.t. where stability is partly due to consistently high recruitment and partly due to adjustments in the growth rate to changes in stock biomass. The higher catches at  $90 \times 10^3$  m.t. are due to the capture of 3-year-olds which is potentially dangerous if cod maturity is a function of length as well as age (Daan 1975). Also some of the improved catch can be attributed to an increase in growth rate. The behaviour of the model in the neighbourhood of  $150 \times 10^3$  m.t. has a sounder biological basis than that near  $90 \times 10^3$  m.t. These two regions are represented by the mid-points of the ascending and descending limbs of the egg production curve; however,  $150 \times 10^3$  m.t. also represents the point of greatest elasticity of growth rate.

#### Relation to production models

The behaviour of the system model under management strategies of constant effort quotas or biomass regulation may be compared with that of general production models (Schaefer 1954, 1957; Pella and Tomlinson 1969; Fox 1970).

Schaefer derived a continuous time model for the dynamics of a fish stock biomass under the assumption of instantaneous response of rate of change of biomass to changes in population density independent of the age composition of the stock. His basic equation was

$$(23) \quad \frac{dB}{dt} = Bf(b) - qXB$$

where  $f(B)$  was a linear function of biomass  $B$ ,  $X$  represented fishing effort and  $q$  the catchability coefficient. Pella and Tomlinson generalized this equation by setting

$$(24) \quad f(B) = HB^m - KB$$

where  $H$ ,  $K$  and  $m$  are constants. Fox (1970) modified Schaefer's model to incorporate a Gompertz growth curve

$$(25) \quad f(B) = K(\ln B_{\infty} - \ln B)$$

Schaefer's model implies a quadratic relation between fishing effort and yield which the extension of Pella and Tomlinson allows this curve to be skewed. Fox's model implies a highly skewed relation between equilibrium yield and fishing effort rising steeply from zero at no effort to a maximum corresponding to a stock size approximately 33% of the maximum and declining slowly with increased fishing effort.

While the relationship between biomass and yield derived from the simulation model (Fig. 15 and 17) resembles those of Pella and Tomlinson and Fox, the relationship between yield and fishing mortality may be described as one half of Schaefer yield curve with yield rising quadratically as  $F$  is increased from 0.0 to 0.6 and dropping discontinuously to zero at some point between  $F = 0.6$  and 0.9.

While the growth rate of fish can respond instantaneously to changes in stock biomass, the recruitment mechanism requires years to compensate to such changes. Thus, an unfished cod stock exhibits cyclic fluctuations which do not arise in the continuous time production models. Agreement with the production models is good in the region of stock biomass between  $150-200 \times 10^3$  m.t. where density-dependent growth is a regulating factor. At low levels of biomass they differ due to complete reliance on recruitment to compensate for biomass fluctuations.

Continuous time models involving structure fluctuations have been studied (Kendall 1949; May 1974), but the fluctuations were infinitesimal and have quite different implications from those

of variation in recruitment which are macroscopic. The absence of such large scale disturbing factors led Fox to conclude that "it is not necessary to place such a tight restriction on the level of fishing mortality as implied by the linear model to maintain an equilibrium yield close to maximum", and although he noted that "beyond the region of maximum equilibrium yield, the reduced population is generally thought to become "sensitized" to adverse environmental conditions", he nevertheless advocated the use of a catch quota system as making the choice between his model and Schaefer's unnecessary. Due to the time lag of the recruitment mechanism of cod the attempt to regulate the fishery by annually removing the maximum yield leads to extreme instability and rapid collapse of the stock. Pella and Tomlinson suggest that the size of the stock be maintained at some intermediate, most productive, level between the maximum population size and extinction through catch or effort restrictions. This conclusion is more circumspect and is in agreement with the simulation results provided a constant catch quota is not adopted.

It is common practice to estimate the parameters of a production model from catch and fishing effort data. In the model of this paper, this method would be satisfactory if effort were held constant for twenty years at each of a series of levels. Unfortunately, observations of catch and effort from a fishery usually form a time series and often involve a trend in effort over the data series. The application of this method of estimation to the simulation model would lead to unpredictable results due to the response time of recruitment. At low levels of  $F$  the cyclic trend of biomass would be more influential than the level of fishing effort for a short time series. If  $F$  were steadily increased from a low level, the relation of catch to effort would be dominated for at least ten years by the initial state of the stock. The use of moving averages of effort would also be unreliable. Thus the "1/2 Schaefer curve" of Fig. 15a might not arise from an analysis of a catch and effort series of, for example, twenty years. Although a general production curve relating yield to fishing effort emerges from the structure of the simulation model, fitting such a curve from catch and effort data is not advisable.

If reliable information on age composition and weight at age is available for commercial catches, it may be possible to estimate the age composition and hence the stock biomass over the history of the fishery using virtual population analysis (Murphy 1967). If a relationship could be found between stock biomass and recruitment and if the response of growth rate to stock biomass were known, then a production curve might be fitted using these relations. It would be wise, however, to manage the fishery at some level of biomass above that promising the maximum yield, at least until the effects of recruitment fluctuations were determined.

Simulation results indicate that management of the cod stock biomass at the point of inflection of the relationship between growth and biomass results in high yield with stable catches. Managing a stock exhibiting density-dependent growth at

this point of inflection has a sound biological basis. It is at this point that the stock is best able to compensate environmental fluctuations with changes in somatic and gonad growth, responding to small perturbations directly as in the general production models and to larger perturbation by changes in egg production and, hence, recruitment. The gain in yield offered by maintaining the stock biomass at a level maximizing the growth rate is obtained at the expense of an impaired ability to respond to the further stress of unfavourable environmental conditions.

Simulations indicate that the cod stock is unable to maintain a production to biomass (P/B) ratio above 0.8 while it is able to sustain a P/B ratio of 0.6 indefinitely. This result suggests that in the absence of more detailed data, it is wise to manage a fish stock at a level below that giving an estimated maximum P/B ratio and the value of 0.6 may be a useful rule of thumb.

#### SUMMARY AND CONCLUSION

It has been demonstrated that adult stock biomass is more important than environmental fluctuations in determining recruitment levels of southern Gulf of St. Lawrence cod. The coarse tuning of the recruitment is achieved by the response of egg production to changes in the growth rate of the adult stock. Fine tuning results from the predation of adult cod on juveniles after they enter the demersal phase. A possible mechanism tending to produce a constant  $l_1$  length is discussed as a stabilizing factor on the biomass of recruiting year-classes.

Consideration of alternatives shows that the most stable and productive level at which to maintain the adult stock biomass is  $150 \times 10^3$  m.t. giving the maximum acceleration of growth in response to perturbations of stock biomass. This stock size is at the point of inflection of the relationship between stock biomass and growth rate.

Cycles and fluctuations in recruitment due to the lag time between spawning and recruitment and environmental fluctuations respectively, proved to be the most important factors in determining the relative merits of different management strategies. Management by constant catch quotas was the poorest strategy considered, resulting in large fluctuations in stock size and fishing effort and leading to a collapse of the stock at lower levels of exploitation than could be maintained by other strategies. Catch quota regulation accentuated the natural cyclic variation of an unfished stock by relating fishing effort inversely to stock biomass. Controlling the fishing mortality rate (constant effort quotas) opposed the natural cyclic tendency of the stock resulting in stability of catch and stock biomass and high levels of yield. Simulation results indicate that control of the spawning stock biomass at  $150 \times 10^3$  m.t. results in high average catches while biomass control at levels

of  $120 \times 10^3$  or  $170 \times 10^3$  m.t. results in fluctuating catches. At low levels of fishing mortality, biomass control appears to produce higher yields with slightly less fluctuation in yield than effort control with the same average biomass.

Yield is increased by allocating more effort to the summer fishery than to the winter fishery. This is due to reduced predation of adults on juveniles and increased stability of spawning stock size. The winter fishery removes age 3 fish before they can spawn.

The relation between fishing effort and yield in the model may be described as one half of a Schaefer yield curve, rising quadratically as  $F$  increases from zero and dropping discontinuously from the peak to zero at high levels of  $F$  due to recruitment failure. Yield per recruit calculations involving levels of  $F$  greater than 0.5 are not a satisfactory basis for management due to the risk of recruitment failure.

It is recommended that the southern Gulf of St. Lawrence cod stock be managed by maintaining the adult stock biomass near  $150 \times 10^3$  m.t. This may be achieved through biomass or effort control with  $F = 0.4$ . The average yield under these policies is in the range of  $40-45 \times 10^3$  m.t., representing a P/B ratio of 0.6.



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APPENDIX I

Correlation matrices of the density-dependent fecundity relationships. Correlation matrix for whole intrinsically linear model in equation (1). Regression was on means.

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Variable	log (Eg+1)	B	B <sup>2</sup>	Tp	Tp <sup>2</sup>
log (Eg+1)	1.0000	-0.3572	-0.4981	-0.3031	-0.2643
B		1.000	0.9844	0.3560	0.3590
B <sup>2</sup>			1.0000	0.4320	0.4248
Tp				1.0000	0.9953
Tp <sup>2</sup>					1.0000

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APPENDIX II

Correlation matrix of the intrinsically linear model of density-dependent larval survival and temperature effects (equation 3).

Variable	log(LR+1)	logIm	logTp	log(Eg+1)	logIm x logTp	logIm x log(Eg+1)	logTp x log(Eg+1)
log(LR+1)	1.0000	0.4377	-0.0375	0.8578	0.4300	0.8336	0.8584
logIm		1.000	0.0512	0.5667	0.9929	0.5887	0.5749
logTp			1.0000	-0.1322	0.1691	-0.1051	-0.0733
log(Eg+1)				1.0000	0.5451	0.9917	0.9981
logIm x logTp					1.0000	0.5694	0.5602
logIm x log(Eg+1)						1.0000	0.9914
logTp x log(Eg+1)							1.0000

APPENDIX III

Correlation matrix of the intrinsically linear model of the density-dependent larval to juvenile relationship (equation 4).

Variable	K/(K-N)	logLR	(logLR) <sup>2</sup>	B	B x logLR	B <sup>2</sup> x logLR
K/(K-N)	1.0000	-0.6781	-0.5433	-0.2994	-0.5874	-0.4974
logLR		1.0000	0.9772	0.5820	0.9627	0.9607
(logLR) <sup>2</sup>			1.0000	0.5465	0.9340	0.9747
B				1.0000	0.7019	0.6534
B x logLR					1.0000	0.9779
B <sup>2</sup> x logLR						1.0000

APPENDIX IV(A)

The mean catch of eggs in the Gulf of St. Lawrence all adjusted to May 20th. The biomass estimates are derived from cohort analysis by subtracting the numbers of fish removed by the commercial fishery between January 1st and May 1st and subsequently multiplying by the mean weights from commercial sampling. Temperatures are of the sea surface taken on cruises in the Gulf of St. Lawrence.

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Year	Eggs/1000 M <sup>3</sup>	Spawning biomass MT	Sea surface temp. °C Grande Rivière, May 20th
1965	8.77	122631	4.4
1966	4.49	122070	4.0
1967	3.31	124886	3.9
1968	1.84	162331	7.2
1969	2.08	157379	5.2
1970	0.88	171281	5.9
1971	0.15	189997	5.8
1972	0.20	167996	4.2
1973	0.67	63085	4.5

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APPENDIX IV(B)

The mean number of larvae/1000,000 M<sup>3</sup> of water strained and the number of days since May 1st to the midpoint of the cruise on which the larvae were collected. The sea surface temperatures are annual monthly mean maximums from Grande Rivière.

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Year	Catch larvae/100,000 M <sup>3</sup>	Number of days since May 1st	Temperature (°C)
1965	18.05	138	13.0
1966	9.23	54	13.1
1967	37.02	83	16.5
	14.14	151	16.5
1968	0.95	89	14.6
	1.34	115	14.6
1969	27.92	44	13.6
	17.02	115	13.6
1970	0.23	81	16.0
1971	11.02*	118	14.4
1972	0.07	118	13.9

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\*this point was considered to be spurious and was not used in the analysis.

APPENDIX IV(C)

The predicted number of larvae on July 20th using equations 1 and 3. Biomass estimates are from cohort analysis and mean weights at age from commercial sampling. Year-class size was also estimated using cohort analysis.

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Year	Larvae/ $10^8$ M <sup>3</sup>	Stock biomass MT 2 yr later	Year-class size $\times 10^{-3}$ at age 2 <sup>+</sup>
1963	8.02	192356	75157
1964	20.84	173024	129814
1965	2421.03	167674	118862
1966	1250.26	188293	68760
1967	1581.25	243904	64969
1968	606.74	222498	108690
1969	818.46	240953	37496
1970	322.11	225252	47437
1971	7.98	151843	91855

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APPENDIX V

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

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Year	Number of cruises	Dates
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	2	May 16-31; Aug. 22-31
1973	1	May 26-June 4

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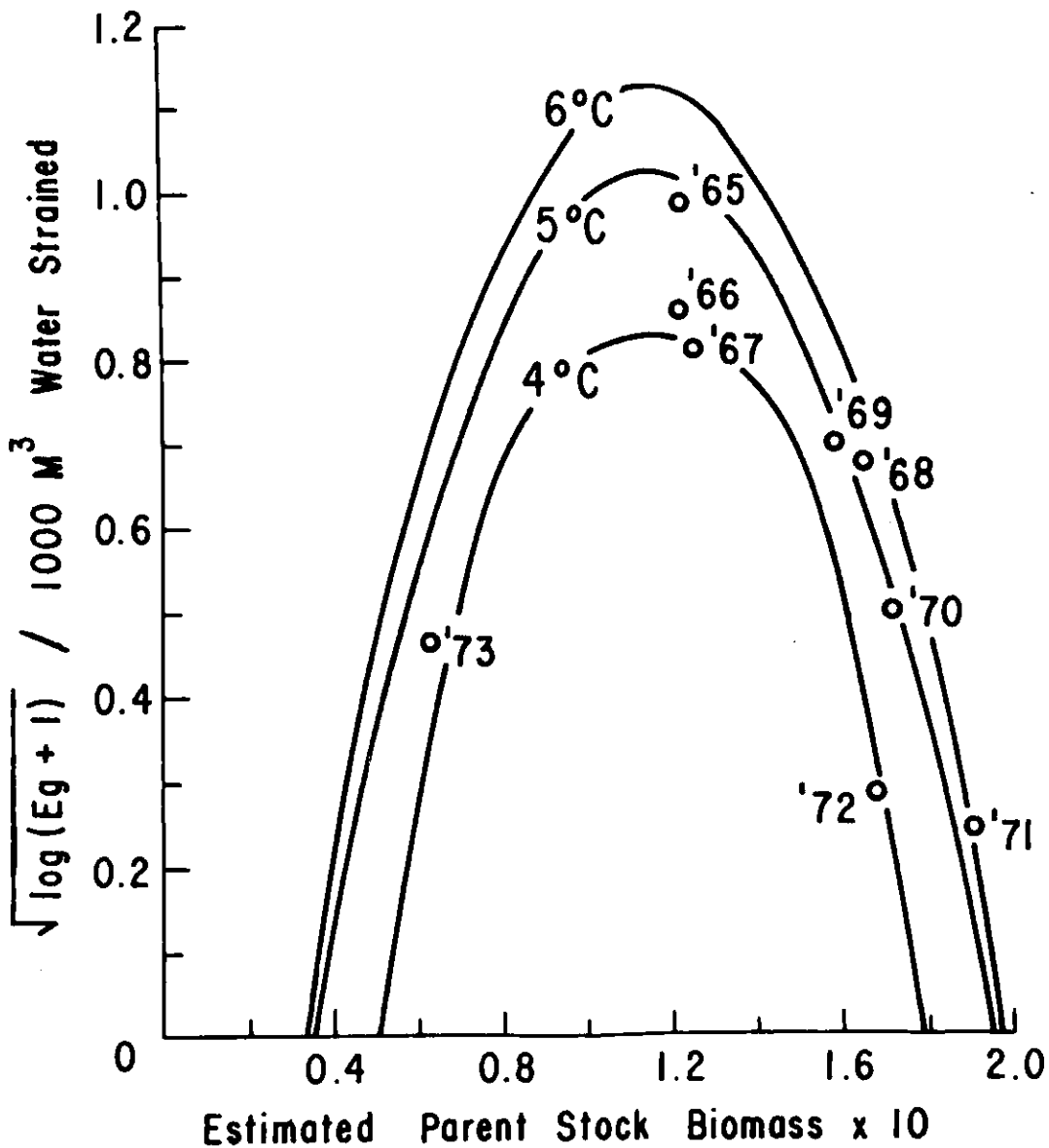


Figure 1. Effect of estimated spawning stock biomass and temperature on the catch of cod eggs/1000 cu m of water strained. Points on the graph have been adjusted to estimate the abundance level on May 20. The corresponding data series is in Appendix IV(A).

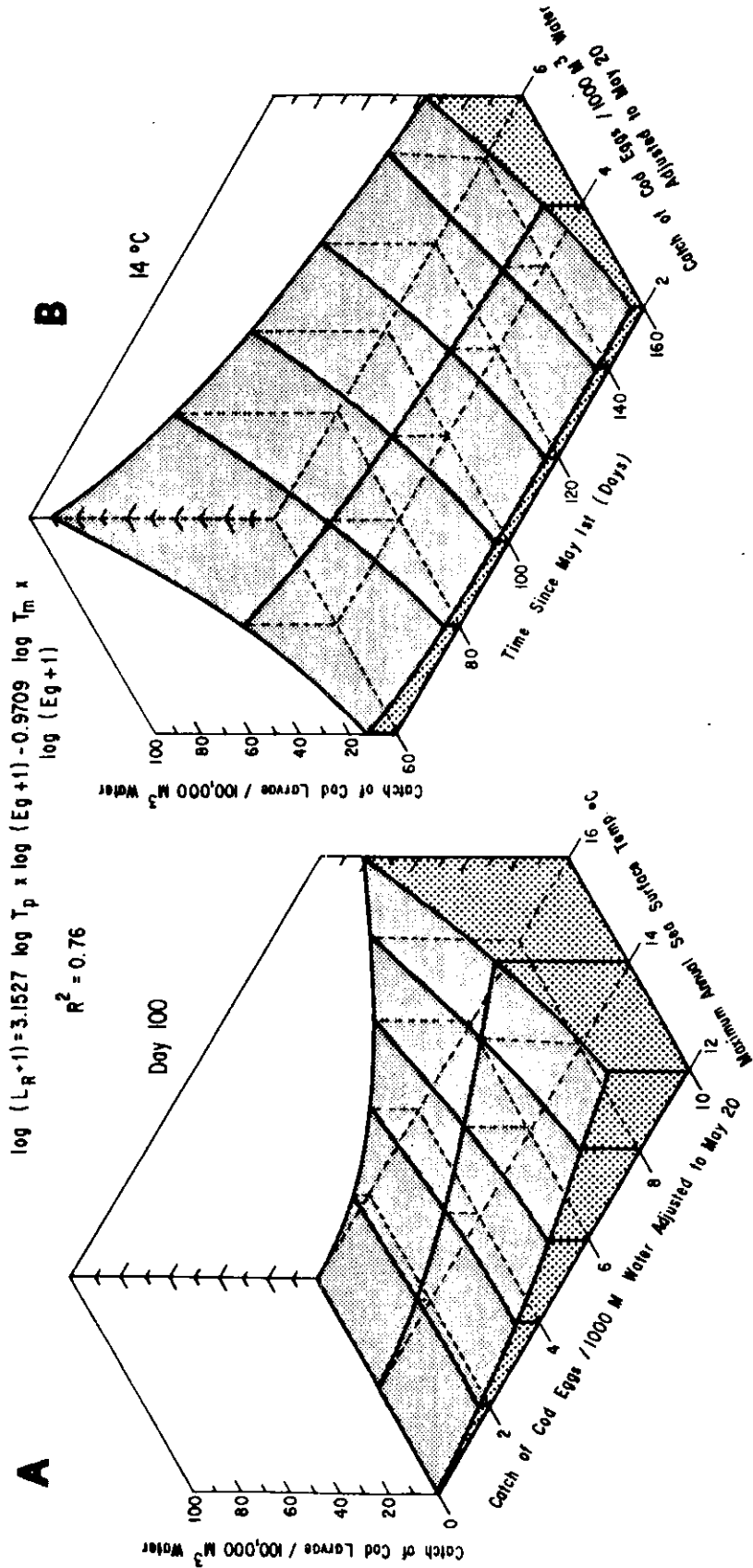


Figure 2. Effect of time, temperature and egg abundance on the catch of cod larvac/1000,000 cu m of water strained. The egg abundance are those adjusted to May 20. The corresponding data series is in Appendix IV(B).



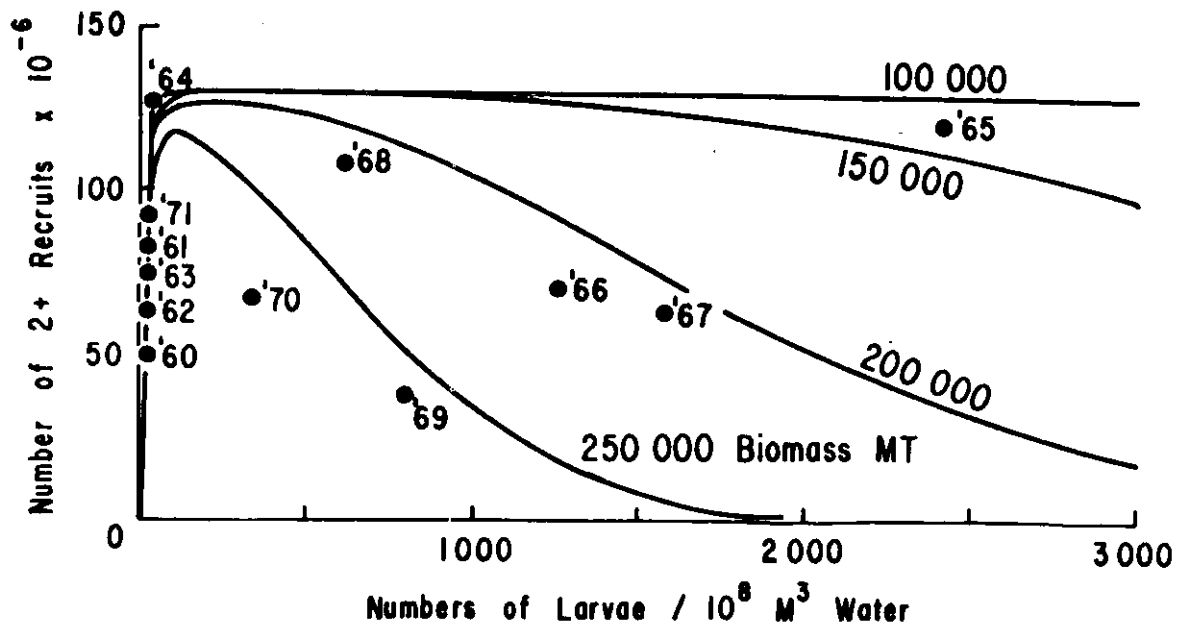


Figure 3. Effect of the interaction of larval abundance and stock biomass  $4^+$  and older on the recruitment of juvenile cod age  $2^+$ . Individual points were predicted using equations (1) and (3) for a larval abundance level on July 20. Only the data series from 1963 to 1971 was used in determining the relationship. The corresponding data is in Appendix (IV(C)).

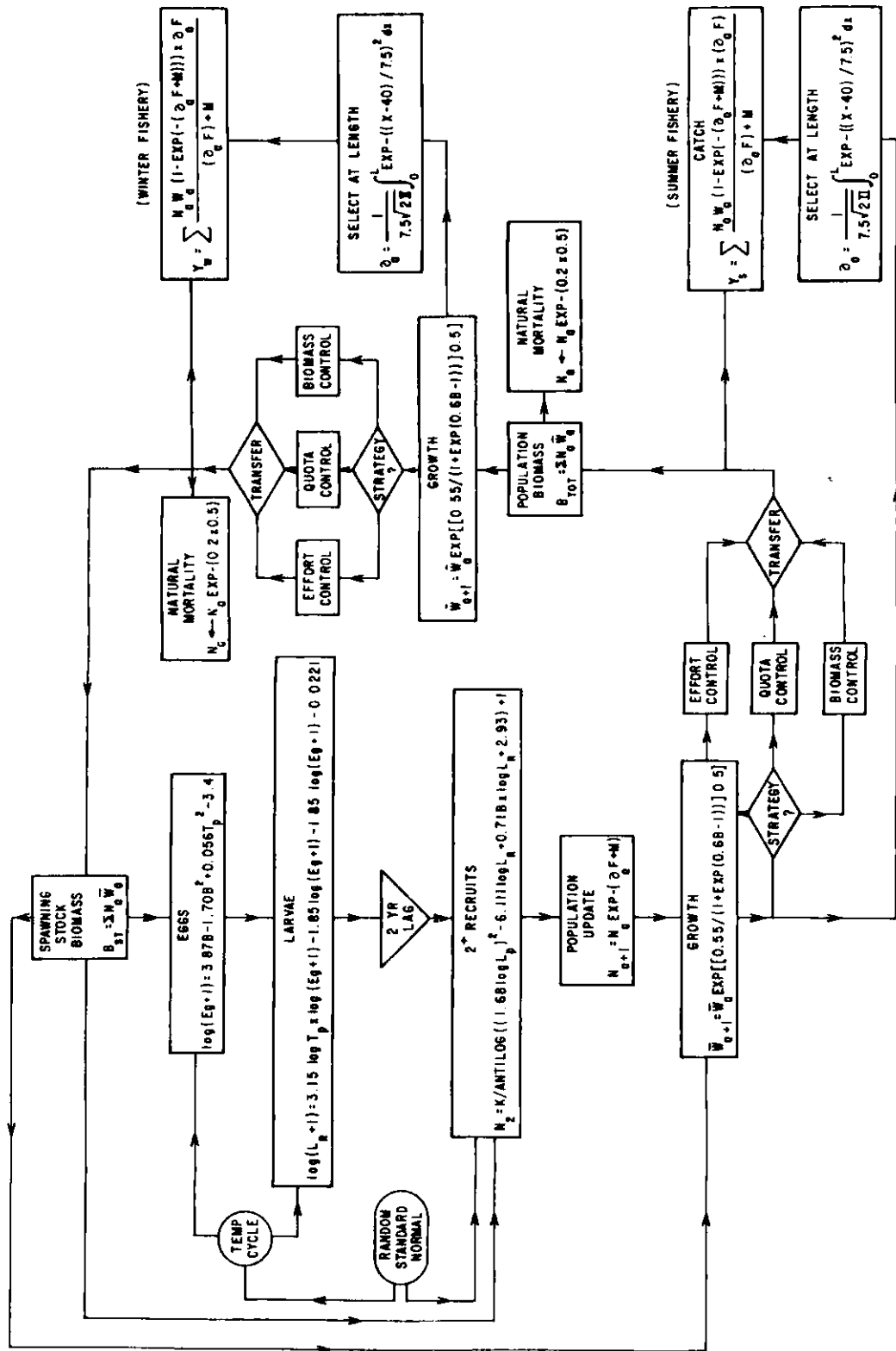


Figure 4. A systems flow chart of the basic cod production system. The model allows for three kinds of management control; they are (1) effort control (2) quota control (3) biomass control. A normally distributed random number sequence was added to the simulation to simulate the empirical effects of a random environment. Selection is by length.

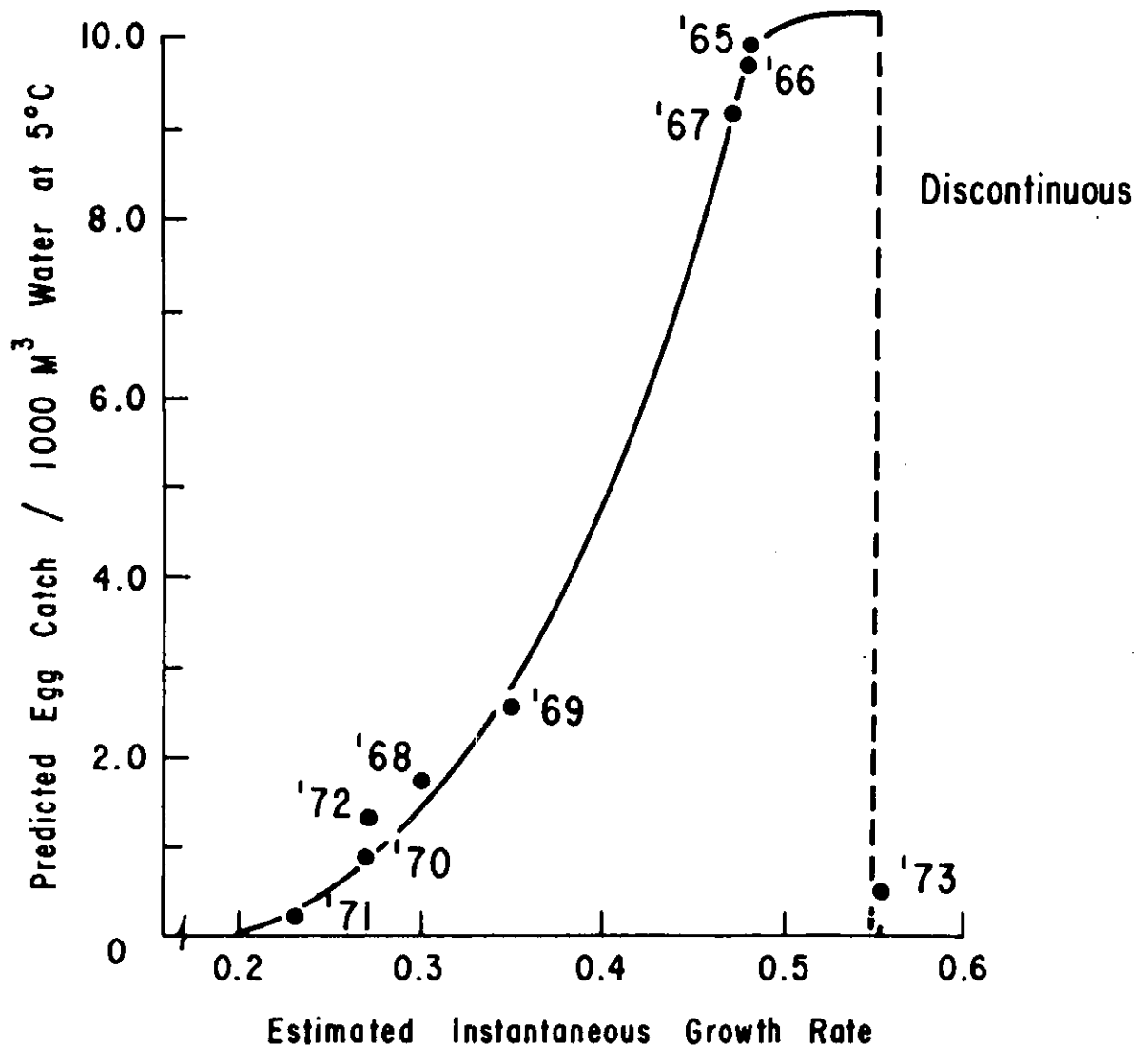


Figure 5. Correspondence of the instantaneous growth rate with production of cod eggs. When the upper asymptotic growth rate is reached, the population is producing the maximum amount of gonad. After this point, the relationship becomes discontinuous, with the number of eggs relying on the number of cod. The curve was fitted by eye. The predicted number of eggs was on May 20 at 5°C while instantaneous growth rate was estimated from its relationship with biomass.

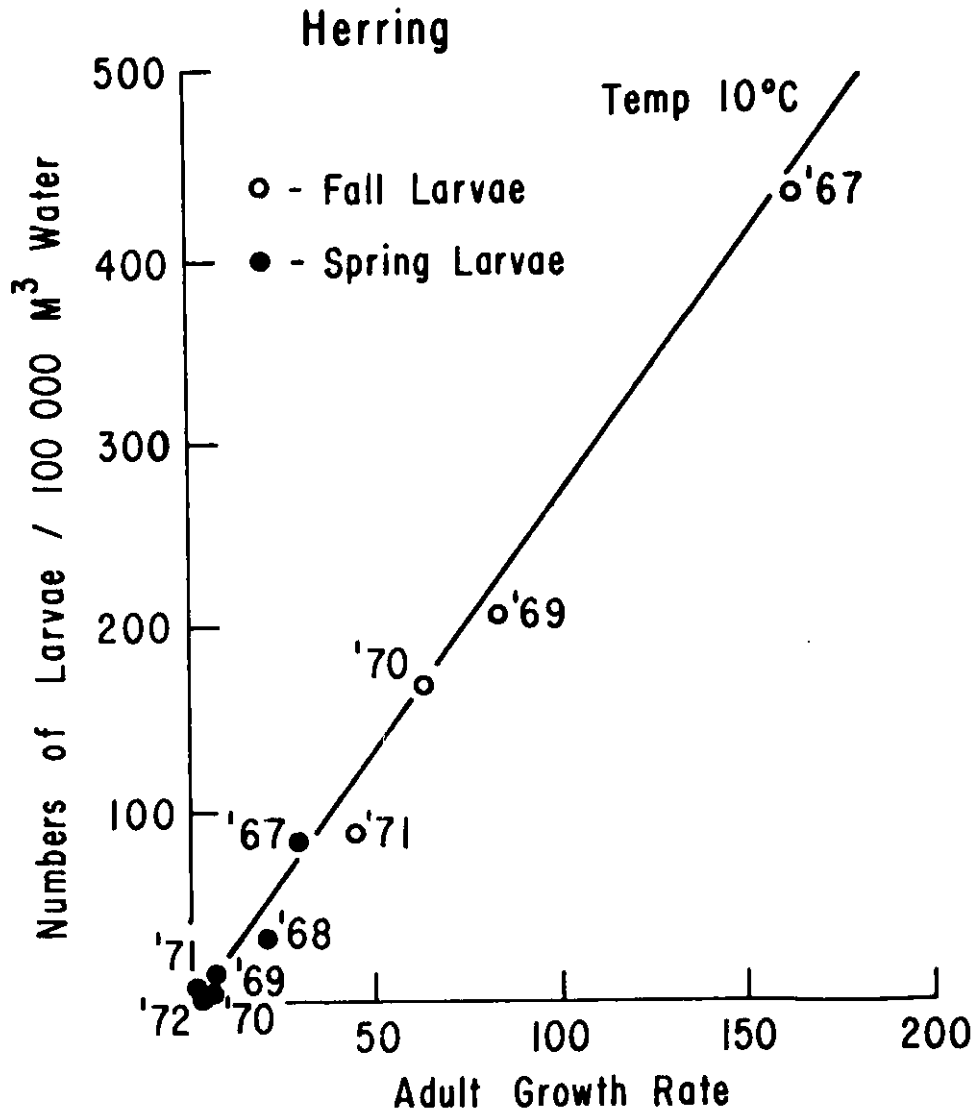


Figure 6. The correlation between the number of stage I larvae and the cumulative adult growth rate i.e.,

$$\sum_{a=1}^{a=n} N_a \times M_a \times G_a$$

where N is the cohort abundance, M is the fraction mature and G is the instantaneous growth rate. Temperature was quadratic so that an optimum could be determined. The points are all adjusted to 10°C. The relationship between cumulative growth rate and larval abundance is the same for both spring and fall spawned larvae.

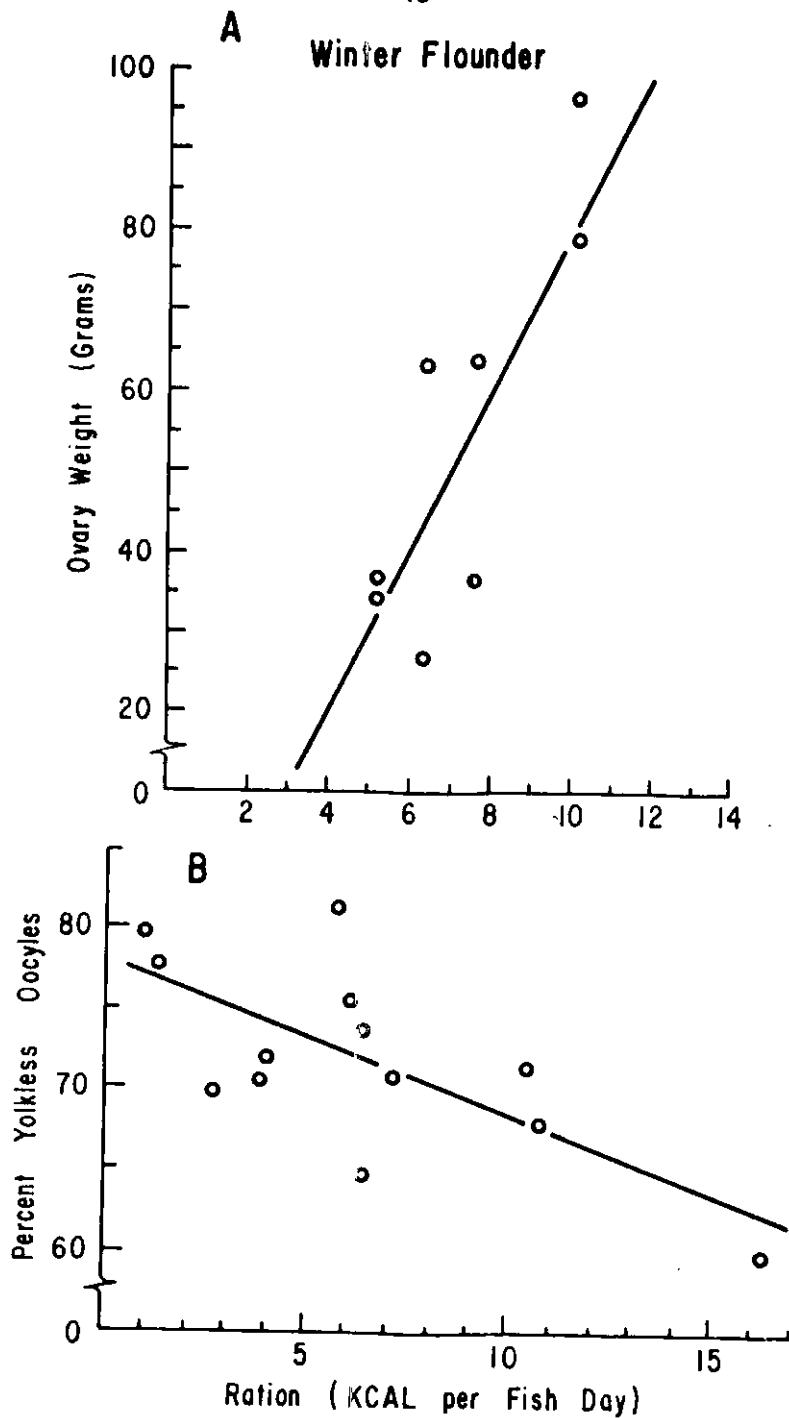


Figure 7. Reproduced from Tyler and Dunn (1975), these two figures show an increase in gonad weight with increasing ration size 7a, a drop in the number of yolkless oocytes (7B).

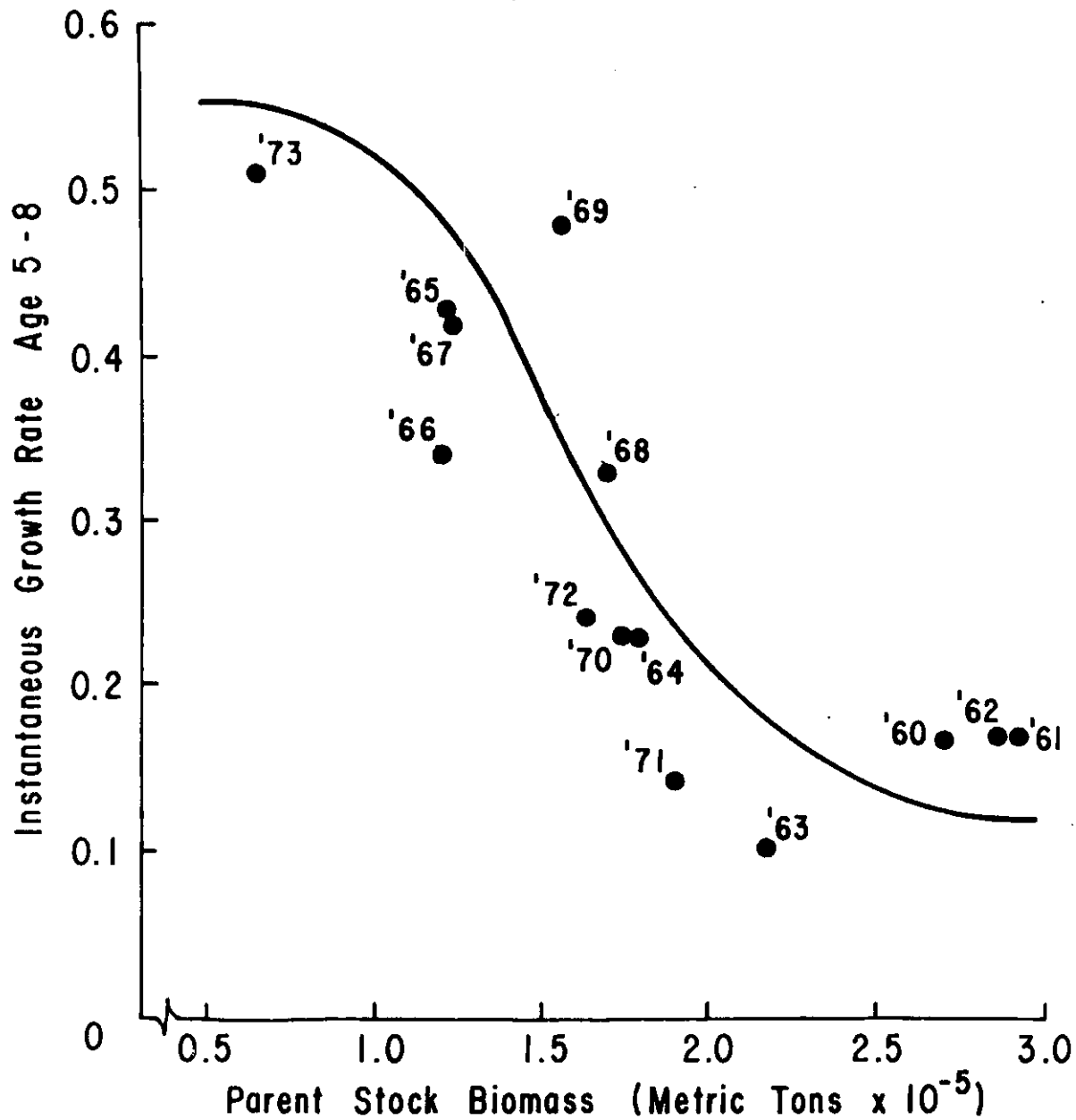


Figure 8. Demonstrates a clear relationship between the summer biomass and the instantaneous growth rate of southern Gulf of St. Lawrence cod. The point of inflection of the curve occurs at  $\approx 1.5 \times 10^{-5}$  mt, at this level of biomass stock can compensate very quickly for changes in biomass.

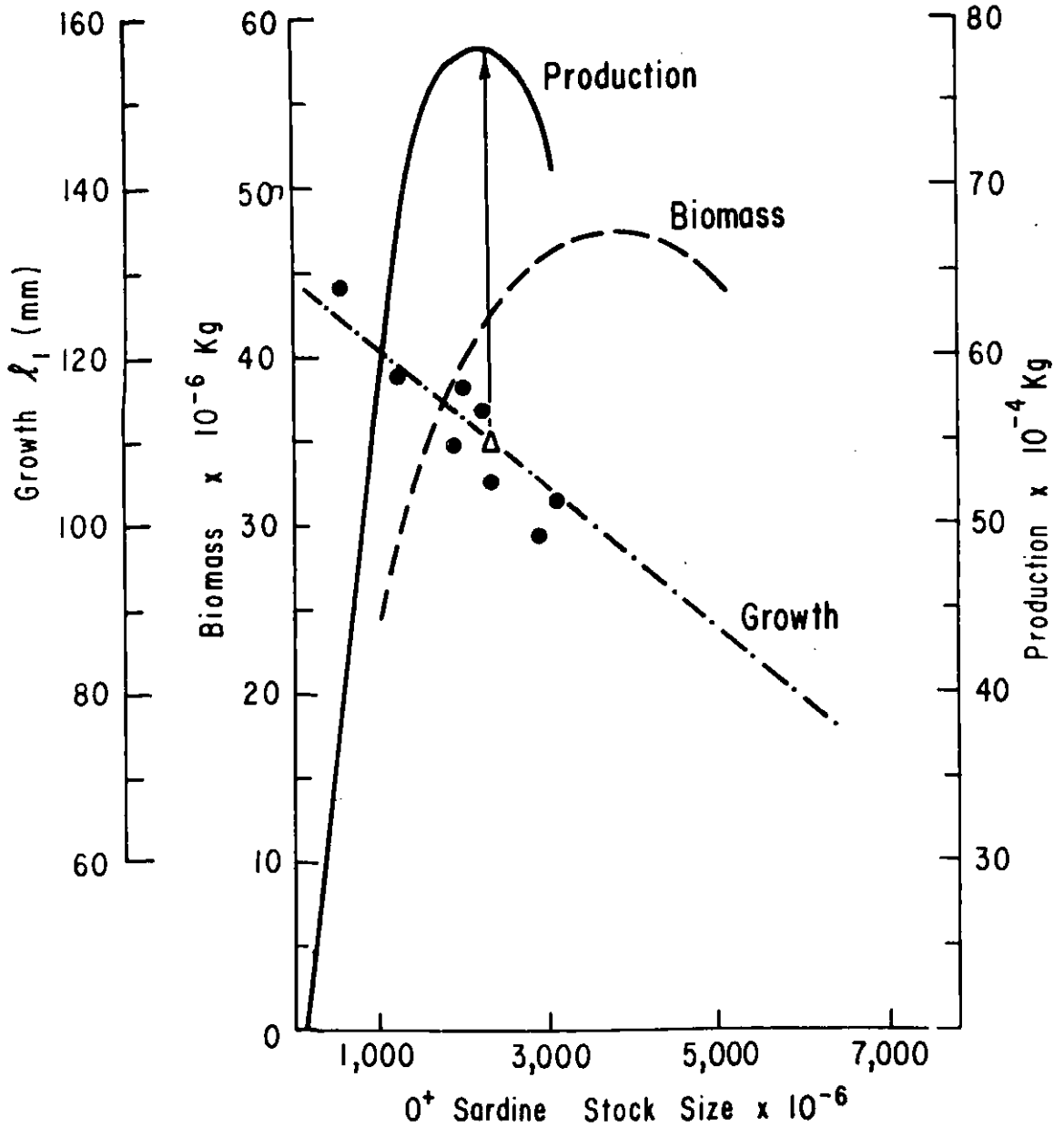


Figure 9. Illustrates the relationship between year class size growth ( $l_1$ ), biomass and annual production. The circles  $\bullet$  represent the  $l_1$  length for given year class sizes. The triangles  $\Delta$  represents the mean of these points which falls directly under the maximization of production. At this point the instantaneous growth equals the instantaneous mortality. The convergence toward this stable point determines the  $l_1$  and year class size, as well as a population stabilizing mechanism.

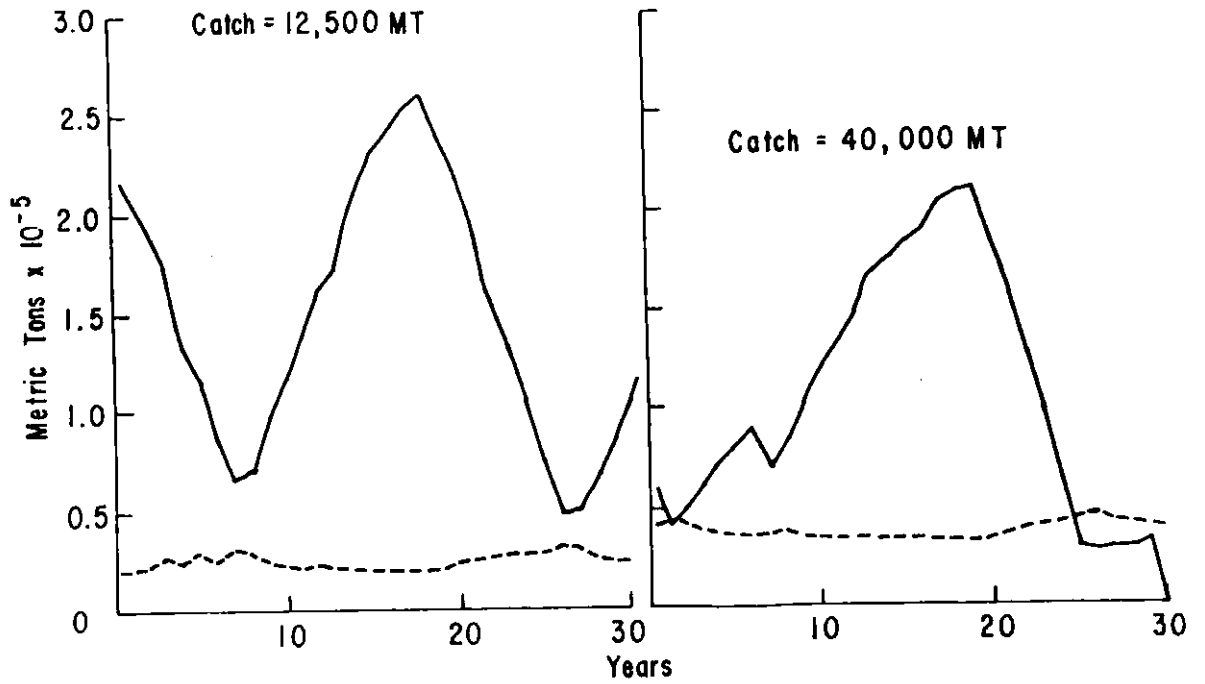


Figure 10. Fluctuations of biomass and catch under two levels of catch quota control. Biomass - solid line, Winter fishery catch - dashed line.



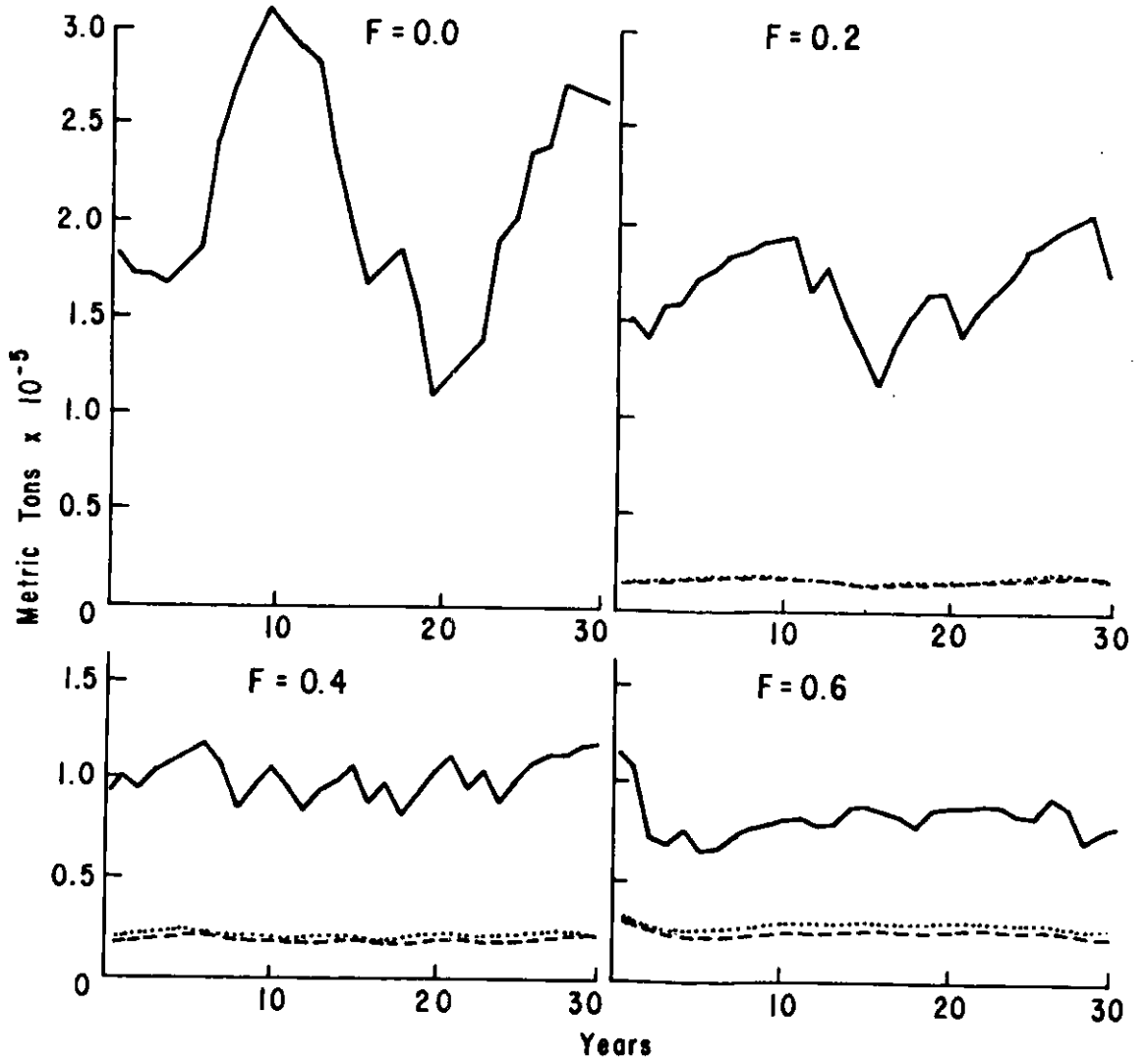


Figure 11. Fluctuations of biomass and catch under four levels of constant fishing mortality rate, equally divided between summer and winter fishing. Biomass - solid line, summer fishery catch - dotted line, winter fishery catch - dashed line.

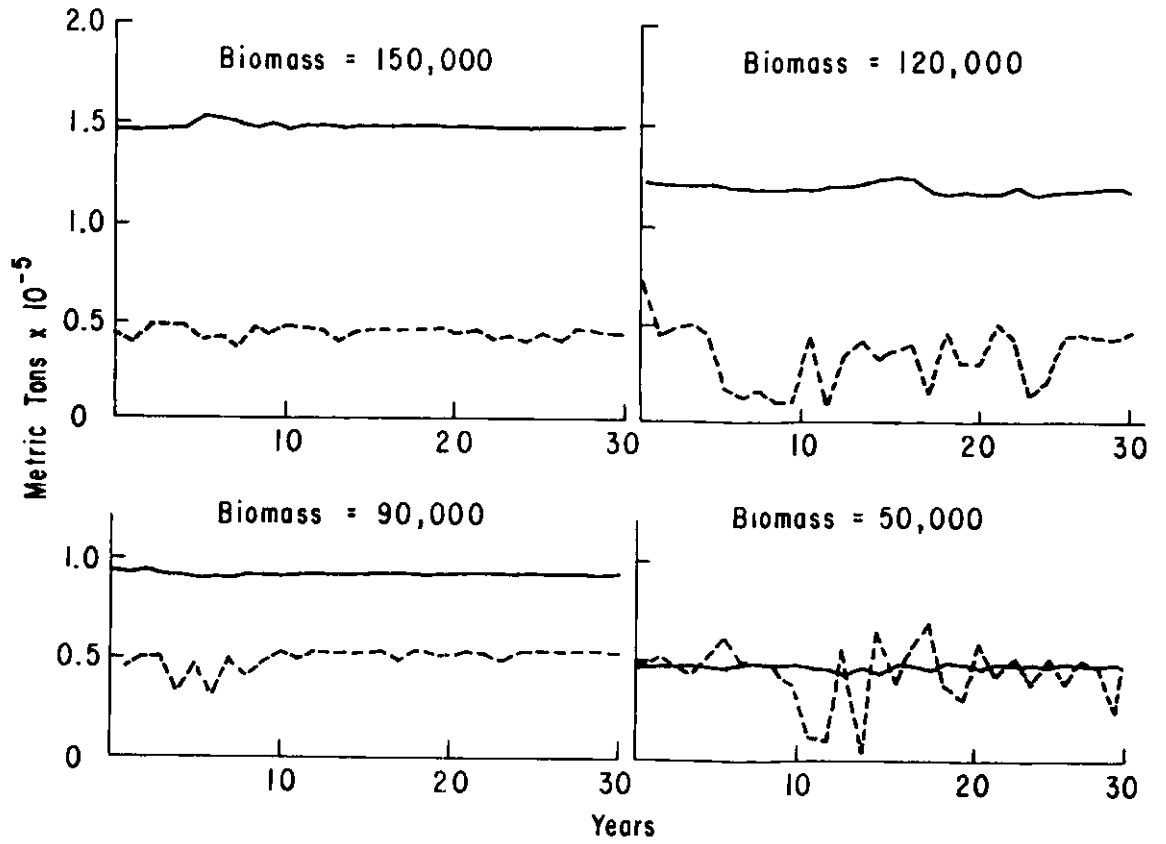


Figure 12. Fluctuations of biomass and catch under four levels of biomass control. Biomass - solid line, winter fishery catch - dashed line.

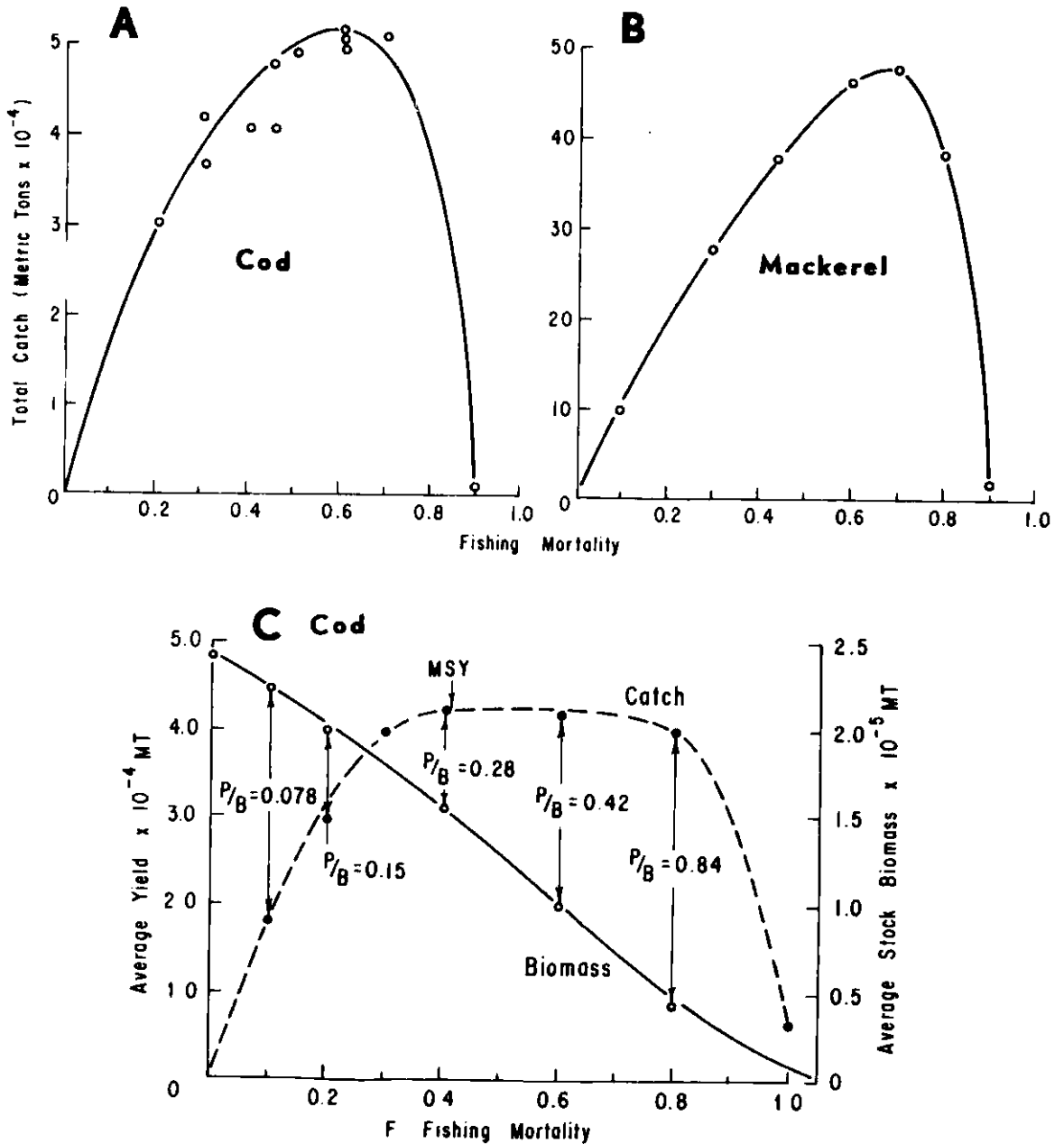


Figure 13. Illustrates the relationship between fishing mortality and catch when the environment is random A, B and when the environment is fixed. When the environment is stable, recruitment at levels of F over 0.4 are nearly constant thus sustaining a high level of catch C. This same result can be achieved by harvesting to a constant biomass. With a random environment, the level of F producing maximum catch is  $\approx 0.6$  for both mackerel and cod, however, the production of mackerel is about 10 times that of cod which is not surprising since cod feed approximately one trophic level below that of mackerel. The mackerel curve is from Lett et al. (1975c). The precipitous side of the curves are brought about by a recruitment failure.

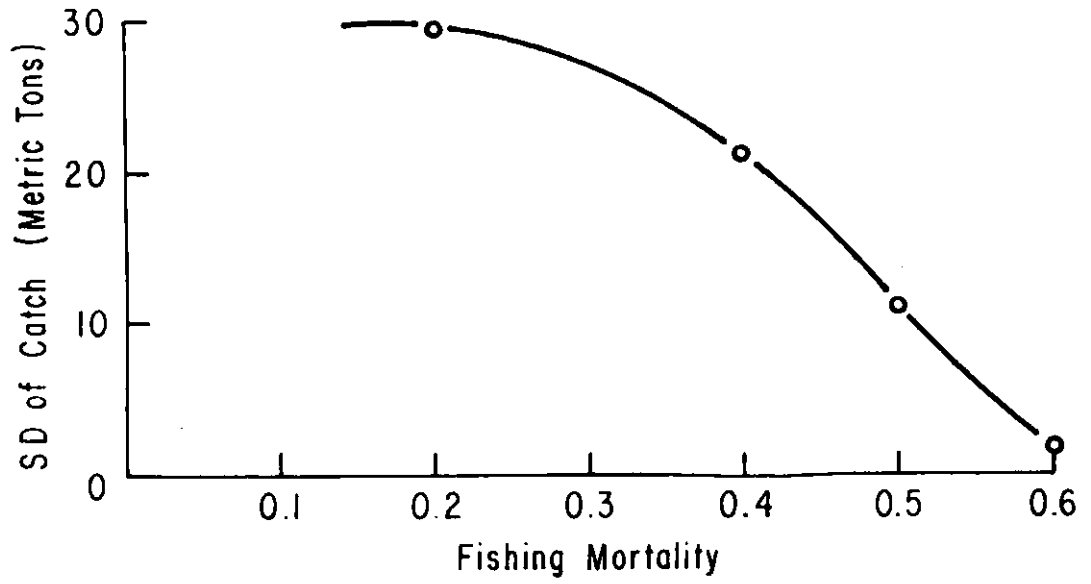


Figure 14. Relationship between controlled level of  $F$  and SD of catch.

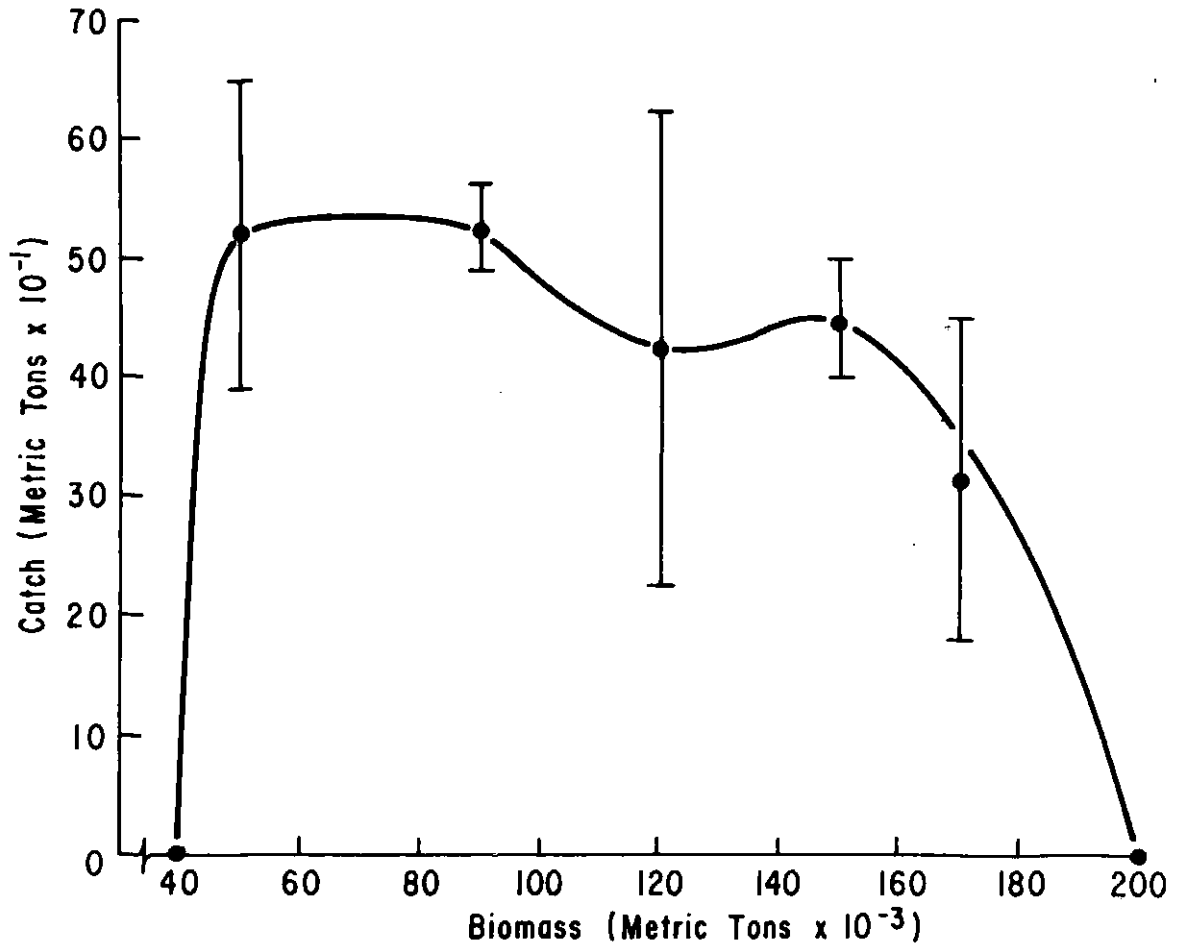


Figure 15. Relationship between controlled level of biomass and average yield. The bars represent one SD in annual catch.