553

A Comparative Study of the Recruitment Mechanisms of Cod and Mackerel, Their Interaction, and Its Implication for Dual Stock Assessment

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553

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A COMPARATIVE STUDY OF THE RECRUITMENT MECHANISMS OF COD AND MACKEREL, THEIR INTERACTION, AND ITS IMPLICATION FOR DUAL STOCK ASSESSMENT[1]

by

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TABLE OF CONTENTS

	Page
Abstract	vi
Introduction	1
Gulf of St. Lawrence cod	1
Northwestern Atlantic mackerel	2
Methods and Results	2
Ichthyoplankton surveys in the southern Gulf of St. Lawrence	2
Estimating the numbers-at-age for mackerel	3
The basic assessment data for cod	4
Catch-at-age	4
Fishing effort	5
Sequential population analysis	6
Research survey data	6
Juvenile surveys and prediction of year-class size	7
Biological data relating to growth and maturity	7
Density-dependent growth for cod	7
Seasonal growth of cod	8
Growth changes in mackerel	8
Density-dependent growth of cod and mackerel in the first year	8
Shifts in maturity with length	9
A Preliminary Analysis of the Bioenergetics of the Recruitment Process	9
Egg production by the adult stock	9
The production of larvae	11
Factors affecting year-class size	12
Construction of the Simulation	13
Results and Discussion	16
The recruitment mechanism	16
General production models and environmental variability	17
Acknowledgments	18
References	18
Tables	22
Figures	32
Appendix 1	45

LIST OF TABLES

Page

Table 1. Cohort analysis, numbers-at-age x 10^6, M = 0.3 for mackerel. Starting values in 1977 are based on a population estimate determined from the egg survey information 22

Table 2. Fishing mortality (F) from cohort analysis, M = 0.3 for mackerel 22

Table 3. Catch-at-age of cod, landed x 10^3 23

Table 4. Fishing effort (f) in trips, catch in metric tons (MT), and catch rates (CUE) for southern Gulf of St. Lawrence cod 24

Table 5. Selection-at-age for the weighted combination of the different gear types, for cod 25

Table 6. Cohort analysis, numbers-at-age x 10^3, M = 0.2, for cod 26

Table 7. Fishing mortality (F) from cohort analysis, M = 0.2, for cod 27

Table 8. Catch rate of 2+ cod caught in groundfish surveys in the southern Gulf of St. Lawrence and 3+ numbers-at-age from cohort analysis 28

Table 9. Catch rate of 2-yr-old cod from groundfish surveys and the abundance of 3-yr-old cod of the same year-class, as estimated by cohort analysis 28

Table 10. Weights-at-age (kg) of cod in 4T(Vn) for January 29

Table 11. Mackerel length-at-age (mm) in Div. 4X during July, August and September of the year indicated 30

Table 12. Weight-at-age (g) for mackerel samples in Subarea 4 fishery during July, August and September 30

Table 13. Observed numbers-at-age of cod estimated from cohort analysis, and estimated values calculated using equation 27 31

LIST OF FIGURES

Page

Fig. 1. Autumn distribution of cod in the Gulf of St. Lawrence determined by fall research surveys between 1970 and 1976. Values are the average kilogram per ton 32

Fig. 2. 3+ cod and 2+ mackerel biomass over time as determined by cohort analysis in this study . . . 32

Fig. 3. Typical cruise track of Gulf of St. Lawrence egg and larval surveys adopted after 1967 . . . 33

Fig. 4. Average distribution of cod eggs in the Gulf of St. Lawrence during the peak spawning period. Units are thousands of eggs per 10^5 m^{-3} water 33

Fig. 5. Distribution of mackerel eggs per square meter of surface water in the Gulf of St. Lawrence . 34

Fig. 6. Selection of different gear types in the southern Gulf of St. Lawrence cod fishery. Curve marked 4.5 refers to trawl selection 34

Fig. 7. Average fishing mortality from cohort analysis age 3-15 cod versus effective effort x 10^3 . . 34

Fig. 8. Relationship between the estimated number of 3+ cod from cohort analysis and CUE 2+ cod caught in the fall of the previous year in the Gulf surveys 35

Fig. 9. Relationship among instantaneous growth rate, biomass and weight showing density-dependent growth in the Gulf of St. Lawrence cod 35

Fig. 10. A cumulative seasonal growth pattern for cod based upon laboratory experimentation by Waiwood (unpubl. data); see text for explanation of relationship 35

Fig. 11. Relationship between 0-group length of mackerel sampled in Div. 4X and year-class size . . . 36

Fig. 12. Maturity ogives for female cod in the Gulf of St. Lawrence between 1959 and 1974 36

Fig. 13. The mean length at maturity of Gulf of St. Lawrence cod as a function of the ℓ_1 growth rate (cm) 37

Fig. 14. The relationship among weighted mean, growth rate of mature cod, and egg catch per mature individual in the southern Gulf of St. Lawrence. The line is computed from equation 20 by using 5°C 37

Fig. 15. Relation between the weighted mean growth rate, $\Delta\hat{W}$, (in g/yr) and the catch of eggs per mature mackerel 38

Fig. 16. Simulated relationship between the number of cod eggs at peak spawning and the numbers of larvae 50 d later. Temperature is varied as in equation 26 38

Fig. 17. Relationship between the catch of 2-yr-old cod in the Gulf surveys and the year-class size-at-age from cohort analysis. Arrows are predicted values based upon the CUE of 2-yr-olds in the Gulf survey 39

Fig. 18. The relationship between observed and estimated year-class size of cod, using equation 28 . . 40

Fig. 19. Relationship between year-class size of cod x 10^7 and larvae for a fixed mackerel biomass and variable cod biomass 40

Fig. 20. Relationship between year-class size in mackerel (0-group) and egg catch from the adult stock. Relationship has been adjusted to a temperature of 16.8°C 41

Fig. 21. Two stock-recruitment curves for mackerel showing effects of variable temperature based on the relationship described by equation 31 41

Fig. 22. Flow chart of system simulation of cod and mackerel fishery 42

Fig. 23. Simulated relationship between change in weight in the current year (ΔW) divided by weight in the previous year (W_{t-1}) 43

Fig. 24. Relationship between mackerel catch and biomass, for different levels of fishing mortality. Mackerel catches and biomasses have been reduced by 15% from simulated values to represent the fishery in ICNAF Subareas 5 and 6. Bars are ±1 SD. (Biomass ■, catch ▲) 43

Fig. 25. Relationship between catch and biomass of cod at three different levels of mackerel biomass . 44

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ABSTRACT

Lett, Patrick F. 1980. A comparative study of the recruitment mechanisms of cod and mackerel, their interaction, and its implication for dual stock management. Can. Tech. Rep. Fish. Aquat. Sci. 988, vi + 45 p.

A continuous dynamic simulation has been constructed describing the interaction of cod and mackerel in the southern Gulf of St. Lawrence. The simulation consists of submodels which describe different portions of the life histories of both species. The data for construction of the submodels came from ichthyoplankton surveys, commercial port sampling, and research vessel cruises. Methodology is described in detail. Catch-at-age, fishing effort data, numbers-at-age, and results from research vessel surveys are included. Biological data related to growth and maturity of cod and mackerel are described. A density-dependent growth relationship is presented for cod in addition to a seasonal growth pattern based on laboratory experimentation. No relationship between growth and biomass for mackerel was found; however, a density-dependent growth relationship could be shown when related to year-class in the first year. The length at which cod mature was estimated from the rate at which they grow in the first year. For mackerel the maturity ogive was found to be a fixed function of length. The catch of cod and mackerel eggs at peak spawning was related to the growth rate of the mature stock and the numbers of mature fish. Sea surface temperature also affected the catch of cod eggs. A relationship was found between the number of cod eggs at the peak of spawning, sea surface temperature, and the number of surviving larvae 50 d later.

A submodel was constructed to describe the recruitment of 3-yr-old cod as a result of mackerel predation on cod larvae, cannibalism by 3+ cod on 0- and 1-group fish, and varying abundance levels of cod larvae. Since data on mackerel larvae are poor, a submodel was created relating the catch of mackerel eggs directly to the year-class size of 0-group mackerel. Temperature was an important variable in this relationship. The simulation was used to look at the general production relationships for both mackerel and cod, and these were used to gain insight into management options for the two species.

Key words: cod, mackerel, recruitment, competition, multispecies management, computer simulation, density-dependent growth

RÉSUMÉ

Lett, Patrick F. 1980. A comparative study of the recruitment mechanisms of cod and mackerel, their interaction, and its implication for dual stock management. Can. Tech. Rep. Fish. Aquat. Sci. 988, vi + 45 p.

Nous avons construit des sous-modèles de simulation dynamique en continu des interactions de la morue et du maquereau dans le sud du golfe Saint-Laurent. Chacun des sous-modèles décrit différentes étapes du cycle évolutif des deux espèces. Les sous-modèles ont été construits à partir de données sur l'ichthyoplancton, d'échantillonnages réalisés dans des ports de commerce et d'expéditions sur des bateaux de recherche. Les méthodes utilisées sont décrites en détail. Les données sur les prises par catégorie d'âge, l'effort de pêche, le nombre de sujets par catégories d'âge et les résultats des expéditions de recherche sont inclus. Nous décrivons les données biologiques ayant trait à la croissance et à la maturité de la morue et du maquereau et présentons une relation décrivant la croissance de la morue en fonction de sa densité ainsi qu'un aperçu de son rythme saisonnier de croissance d'après des manipulations de laboratoire. Chez le maquereau, aucune relation entre la croissance et la biomasse n'a été trouvée; toutefois, on peut montrer une relation entre la croissance et la densité en fonction de la catégorie d'âge, pour le poisson d'un an. La longueur à laquelle la morue arrive à maturité a été estimée à partir de son rythme de croissance au cours de la première année. Chez le maquereau, la courbe des fréquences cumulées de la maturité serait une fonction fixe de la longueur. Le numbre d'oeufs de morue et de maquereau capturés au moment où le frai est à son maximum a été mis en relation avec le rythme de croissance du stock adulte et du nombre de poissons adultes. La température de surface de la mer a aussi influé sur la capture des oeufs de morue. Une relation a été trouvée entre le nombre d'oeufs de morue au maximum du frai, la température de surface de la mer et le nombre de larves survivantes 50 jours plus tard.

Un sous-modèle a été construit pour décrire le recrutement de la morue de 3 ans à la suite de la chasse des larves de morue par le maquereau, du cannibalisme par les morues d'âge 3+ sur le groupe d'âge 0 et 1 et de l'abondance variable des larves de morue. Comme les données sur les larves de maquereau sont peu nombreuses, nous avons construit un sous-modèle établissant un rapport direct entre la capture d'oeufs de maquereau et la grosseur de sa classe d'âge 0. Dans ce rapport, la température constitue une variable importante. La simulation a servi à examiner les rapports généraux de production du maquereau et de la morue, et ceux-ci ont servi à mieux apprécier les options de gestion des deux espèces.

INTRODUCTION

To understand how different species of fish interact with each other and with their environment, it is usually necessary to model the system. There are different levels at which this can be approached, each of them revealing different functional attributes of the system. At one end of the spectrum of possible models are those of Dickie (1972), Horwood (1976), and Pope (1976), which consist of a few equations that interact mathematically. Dickie attempts to explain large portions of ecosystem structure by rather simple equations while Pope and Horwood model only the production of the fish species of interest. At the other end of the spectrum, Andersen and Ursin (1977) have produced a noteworthy model involving a detailed simulation of the North Sea ecosystem, considering the interaction of a number of different trophic levels. Although both these modeling approaches have their merits, more knowledge about species interaction can probably be gained by taking an intermediate point of view, considering more of the biology than Pope (1976) and Horwood (1976) and less of the minutiae dealt with by Andersen and Ursin (1977). One such model was produced by Riffenburgh (1969), which considered the flow of energy from one ecosystem composed of the Pacific sardine (*Sardinops sagax*), the northern anchovy (*Engraulis mordax*), their competitors, their predators, and their prey, using a stochastic approach.

All of the above examples fail to detail the early life history of the different fish species. Indeed, it is during the early life history or recruitment phase that most of the interactions between and among different species occur. Lett and Kohler (1976) considered the interaction of Atlantic mackerel (*Scomber scombrus*) and herring (*Clupea harengus*), making a detailed examination of the recruitment phase and the way individual mechanisms interlink to make the population dynamics of herring largely dependent upon fluctuations in the abundance of mackerel. The Lett-Kohler model, and the model to be presented here, will deal with four life stages of fish: eggs, larvae, juveniles, and adults. Within each of these stages we deal with density-dependent processes of growth and mathematical representations of mortality.

There is also a problem in the scale of the models attempted. There is little gained by constructing a simulation of a system in order to understand it, only to find that the model becomes so complex that it, too, is not tractable. The best procedure is to construct submodels dealing with portions of the system, understand the details of these models, and then give them to the mathematicians to be generalized and incorporated with other submodels for the study of the system at a different scale, where the initial detail has less relevance. The simulation to be presented in this paper will consist of a number of submodels dealing with different portions of the life history of cod (*Gadus morhua*) and the Atlantic mackerel.

GULF OF ST. LAWRENCE COD

Cod have been fished in the Gulf of St. Lawrence for more than a century during the ice-free months. Prior to the mid-forties, the fishery was primarily by baited hook or jig, and it was not until the introduction of foreign otter trawls that any significant changes took place. The introduction of foreign otter trawls in the mid-fifties also had a major effect on the fishery.

This cod stock, delineated in three tagging studies, has been shown to occupy only ICNAF Division 4T and Subdivision 4Vn (McCracken 1959; Martin and Kohler 1965; Kohler 1975). There are two main areas where the fish appear to congregate and where the fishery is concentrated: first, the Magdalen Shallows between the Magdalen Islands and the Gaspé (Fig. 1) and, second, the edge of the Laurentian Channel off the northwest coast of Cape Breton. The annual migratory pattern is from the Magdalen Shallows in the fall to the area of dense winter concentration in the so-called Sydney Bight. In May, following breakup of the ice, they migrate to spawn in the highly productive shallows of the southern Gulf (Paloheimo and Kohler 1968). Increases in fishing effort were associated with increased foreign interest in the winter fishery but recently the winter fishery has been closed to foreign vessels and, in addition, there has been a reduction in domestic effort.

Between 1936 and 1953 the average catch from the 4T cod fishery was approximately 33 000 metric tons (MT), a figure which at the time was thought to be optimal for a sustained fishery, based upon my conversations with some of the older fishermen. The fishery would probably have continued at this level if it had not been for the onset of an epizootic disease of the pelagic fish stocks, a systemic fungus disease described by Sindermann (1958) that began in 1950 and reached a peak in 1954-56.

The epizootic disease had catastrophic effects on the Gulf of St. Lawrence ecosystem by destroying a large portion of the herring and mackerel stocks. From a scientific point of view it was rather opportune since this violent perturbation resulted in a wide fluctuation in the stock-dependent variables controlling the fish production systems. Furthermore, the 'die-off' of the pelagic fish biomass facilitated the growth of cod (Kohler 1964), improved their recruitment (Lett and Doubleday 1976), and generally led to an increase in the exploitable cod biomass (Fig. 2). During the period between 1954 and 1957 there were four year-classes of age 3 cod in excess of 10^8 individuals. Such changes have also been noted in the North Sea where the increase in cod biomass is attributable to the decline in the biomass of pelagic fishes, notably herring (Jones 1976; Steele 1978).

In the late fifties the pelagic fish biomass in the Gulf of St. Lawrence began to recover, with two large herring year-classes in 1958 and 1959 produced in conjunction with the relatively large 1959 year-class of mackerel. As the pelagic biomass increased the 3+ cod biomass declined rapidly from a high of 560 000 MT in 1955 to a low of 156 000 MT by 1967, in part due to a substantial increase in fishing effort. During 1955-67, the average annual catch from the southern Gulf stock was 78 000 MT, with a peak catch in 1956 of 110 000 MT.

However, a preliminary analysis of the data showed that the management of this stock is only partially dependent on the manipulation of fishing effort. Indeed, the calculation of fishing mortality between 1960 and 1975, as indicated in subsequent calculations, shows that the exploitation rate is much lower than has been experienced by the other cod stocks fished in sustainable manner. The critically low 1973-75 level of cod stock biomass

is probably more the result of interactions with other fish stocks than the effects of single species exploitation.

NORTHWESTERN ATLANTIC MACKEREL

The Atlantic mackerel stock that migrates over the eastern seaboard of North America has been exploited since the 1960's. Statistics from the early 1800's indicate that the stock has fluctuated widely with declining catches from time to time while fishing remained intense (Sette and Needler 1934). Sette (1931) showed that a sharp increase in United States catches in the mid-1920's was the result of recruitment of the strong 1923 year-class.

Recent tagging experiments (Beckett et al. 1974; Moores et al. 1974; Parsons and Moores 1974; Stobo 1976) confirm that migrations may extend from Labrador (Parsons 1970) to North Carolina (Sette 1950). The stock is thought to be made up of two spawning components: the southern component which begins spawning in the vicinity of Long Island gradually moving north into the Gulf of Maine, and the northern component which spawns in the southern Gulf of St. Lawrence. Spawning stock separation based on biochemical and meristic techniques (MacKay 1967; MacKay and Garside 1969) is not great and indeed the actual biomasses of the northern and southern component are a contentious issue. Based upon work of MacKay (1973) and Lett and Marshall (1978), Anderson and Paciorkowski (1978) suggest that between 60 and 70% of the overall mackerel stock may spawn in the Gulf of St. Lawrence. The present study supports the validity of their suggestion for the late sixties but the proportion may be different in more recent years.

The mackerel population overwinters along the edge of the Continental Shelf between Sable Island and Cape Hatteras and then migrates northeasterly and toward shore in the spring into the two spawning areas. The peak of spawning occurs in late April-early May in the Long Island-Gulf of Maine contingent and late June-early July in the Gulf of St. Lawrence contingent. The actual peak of spawning corresponds closely with surface water temperatures of 12-13°C in the Gulf of St. Lawrence (Lett and Marshall 1978).

Recruitment of mackerel is highly variable and seems to depend primarily on sea surface temperature during larval growth (Lett et al. 1975b; Winters 1976; Lett and Marshall 1978). This particular subject will be one of the main topics in this paper. Furthermore, because of the high instantaneous natural mortality rate (0.3, Anderson and Paciorkowski 1978), fluctuations in recruitment lead to dramatic changes in stock biomass. These changes in stock biomass are critically important to the management of the Gulf of St. Lawrence fish (Lett and Kohler 1976).

METHODS AND RESULTS

ICHTHYOPLANKTON SURVEYS IN THE SOUTHERN GULF OF ST. LAWRENCE

Since 1965 an investigation of the distribution and abundance of eggs and larvae in the southern Gulf of St. Lawrence has been undertaken. The major objective was to develop indices of prerecruitment for groundfish species, but it was found that similar information could easily be collected for pelagic species such as herring, mackerel, and capelin. For detailed account of these surveys see Kohler et al. (1974, 1975, 1976). All cruises extended over the Magdalen Shallows with some crossing the Laurentian Channel into St. Georges Bay, Newfoundland (Fig. 3).

Several different gear types were used on the cruises conducted by three Canadian research vessels: *HARENGUS*, *E.E. PRINCE*, and *A.T. CAMERON*. At all times, a 1-m diameter standard net was towed at the surface. The mesh size was Nitex Pattern #471 (15 meshes cm^{-1}). The net was towed so that only the upper surface of the forward hoop appeared just above the water line for 30 min at a range of speeds between 3.7 and 5.5 km hr^{-1}. At the center of the mouth, a TSK (Tsurumi Seiki Kosakusko Co. Ltd.) flowmeter registered the amount of water strained per tow. At times a meter net was also towed at 15-m depth for the same time and speed as the surface tows. Although no closing devices were used on this net, this was not expected to affect the quantitative value of samples.

A modified Isaacs-Kidd (IK) trawl (Isaacs and Kidd 1953) was hauled from as close to the bottom as practical to the surface on an oblique track, the net being raised at 5-min intervals for the 30-min hauling duration. The IK trawl used was 1.82 m with 0.64-cm and 0.32-cm lining and a Nitex Pattern #471 codend. It was also fitted with a 1.22-m paravane depressor. Depth was originally monitored with a clinometer, and later by a Type 102 Benthos Acoustic Telemeter and Oceansonic Model OSR-119T Precision Sonar Recorder. Towing speed was at 0.3 km hr^{-1}.

In 1966 and subsequent cruises, a neuston net (David 1965), modified by M. R. Bartlett of Woods Hole Oceanographic Institution, was used. The mouth of the net was 33 cm by 99 cm and the overall length 6.17 m. The mesh was Nitex Pattern #1179 (6.7 mesh cm^{-1}). This net was hauled for 30 min at 9.3 km hr^{-1} in conjunction with each Isaacs-Kidd oblique tow.

Bongo nets and Miller samplers were used in the 1969 subsequent surveys. These two gear types were towed in conjunction with the meter nets at 4.63 km hr^{-1} for 30 min. The Miller samplers (usually five) were all hauled on the same wire with a 159-kg weight or Braincon V-fin depressor holding the towing warp at about a 45° angle. Angles were measured every 5 min. The samplers on the wire were spaced 9.15 m apart.

The standard 61-cm diameter Bongo net was hauled, using an oblique tow with the first step being as close to the bottom as possible. This has been since changed to a continuous oblique haul with the maximum depth being 100 m. The mesh size on both the Miller samplers and Bongo nets was #471 Nitex.

At the end of each tow, the nets were washed down with salt water to rinse all organisms caught in the net meshes into the plankton-collecting bucket at the end of the net. This ensured that the total sample was saved and prevented contamination of further tows. Flowmeter readings on the inside and outside of the nets indicated if the nets were clogging. The samples, after extraneous plant material and flotsam were picked out, were preserved in 5% formalin for identification and sorting.

Eggs and larvae of all species were sorted and identified, often counted and sorted by developmental stage, but were rarely measured unless for a special project. Early stages of gadoid eggs are almost impossible to differentiate; however, larvae can be separated on the basis of irregularities in pigmentation (Bigelow and Schroeder 1953). When there was doubt concerning the species to which the eggs belonged, some were incubated, hatched and the larvae identified.

Each year at least one cruise was designed to coincide with peak cod spawning in the Gulf of St. Lawrence. Figure 4 shows the average distribution of cod eggs, identifying at least four stock components making up the entire southern Gulf of St. Lawrence cod stock complex. The cruise, starting in the Sydney Bight area and working north through the southern Gulf, usually samples these relatively isolated spawnings at their peak (Kohler et al. 1974, 1975, 1976). The spawning period for cod in the overall Gulf begins in early May, reaches a peak around May 20, and ends by June 15.

All cruises subsequent to spawning caught cod larvae and, since in some years cruises were extended into October, the progressive decline in the catch of cod larvae could be easily monitored.

All the samples were adjusted so that they corresponded to the straining of 100 000 cu m of water. For eggs the estimates from the Miller and standard meter nets were very similar; however, estimates from the obliquely hauled gear were an order of magnitude lower. Because of the small mouth diameter (10.8 cm) of the Miller samplers, they were not efficient at sampling free-swimming larvae, and in these cases the meter and Bongo samplers were much more useful. For the larger cod larvae and juveniles, the Isaacs-Kidd was the most efficient sampler.

Temperature data were available from Grande-Rivière on the south shore of the Gaspé peninsula, Entry Island (which is one of the Magdalen Islands), and from research cruises. Cruise temperatures are similar to those collected at Entry Island and correspond well with Grande-Rivière if the year is broken up into bimonthly segments. In the cod study, Grande-Rivière temperatures are used while the mackerel study used Entry Island temperatures.

ESTIMATING THE NUMBERS-AT-AGE FOR MACKEREL

Because of the difficulty of calculating numbers-at-age for a mackerel population (Anderson and Paciorkowski 1978; Lett and Marshall 1978), I have tried to develop an alternate technique for estimating the present stock size, based upon egg surveys in the Gulf of St. Lawrence. The egg catches in 1969, 1976, and 1977 were used.

Cruises corresponding with the peak of mackerel spawning were conducted in 1967, 1968, 1969, 1976, and 1977. In 1967 the cruise did not cover the entire southern Gulf and is not useful for estimates of the total number of eggs spawned. However, it has some value as an index.

The Miller samples were used to estimate the percentage of eggs at each of the depths sampled. The catch of eggs at the surface by the meter net per 1 000 000 cu m of water was then prorated over depth by the percentage composition determined from the Miller samplers. By integrating (using a planimeter) the number of eggs under a square meter of surface could be calculated. This estimate was then expanded to an area which surrounded each station. These areas were delineated by drawing a straight line between adjacent stations and then constructing a perimeter around the station by joining lines that are orthogonal to the midpoint of the lines between stations (Fig. 5). The size of each area depended on the number of stations in given locations. The area around stations on the margin of the grid cannot be defined objectively; thus a straight line was drawn to minimize the area encompassed by that station. Surface areas were found with the use of a planimeter and the total number of eggs under a square meter was multiplied by this value.

The eggs at each station were all staged according to Worley's (1933) classification. For those eggs that were not stage 1, it was now necessary to estimate the number that had disappeared during the time spent between stage 1 and their present stage. This calculation would give four estimates of the number of stage 1 for some instantaneous time during the spawning cycle.

The number of hours that eggs would spend in each stage was 30, 75, 50, and 20 for stages 1-4, respectively, based upon the interpretation of Worley's (1933) data. A daily mortality rate of 0.4 (D.M. Ware, pers. comm.) was used to estimate the daily loss of eggs in each stage. This mortality rate was developed from studies of patches of mackerel eggs in the southern Gulf of St. Lawrence. Back calculations for each sampling date at each station thus gave the daily production of eggs for four different days at that location. The four estimates of the number of stage 1 eggs at each station were then averaged and these average values were summed to give an overall estimate for the southern Gulf of St. Lawrence. This average value for the entire cruise was then assumed to represent the number of eggs spawned at the midpoint of the cruise.

Recent studies (Lett and Marshall 1978; Ware 1977; Lockwood et al. 1978) have shown that the spawning cycle of mackerel approximates a normal curve. The total area under this curve then is the total egg production, and this can be calculated if one point on the curve is accurately known, in addition to the mean date of spawning and the standard deviation of the cycle. The spawning cycle curve was constructed from ichthyoplankton survey data in 1967, 1968, 1969, 1976, 1977 and 1978. It was found that 95% of the total area under the mackerel spawning cycle occurred between 32 and 40 d (see Appendix 1). This range corresponded to a standard deviation which could vary between 8 and 10 d. Ware (pers. comm.) calculated the duration of spawning in St. Georges Bay, a small bay in the southern extreme of the Gulf of St. Lawrence where a portion of the same stock of mackerel spawn, to be approximately 40 d. These 40 d also corresponded to about a standard deviation of 10 d. Given the above information, the standard deviation for the mackerel spawning cycle was fixed at 10 d for further calculations. An analysis was performed to see how sensitive estimates of the total egg production were to a standard deviation varying between 8 and 10 d (see Appendix 1). The estimate of the total number of eggs will increase by 16% when the standard deviation is decreased by 2 d. Since the cruises for mackerel eggs last for only 7-10 d, the peak spawning period may be missed by a few days.

Therefore, it is necessary to find a way of correction for the possibility that the peak spawning date may be slightly over- or underestimated.

Mackerel spawning is highly temperature-dependent with peak spawning occurring at about 12°C (Lett et al. 1975b). Thus temperature is probably the best variable to which to relate egg production, over time. The temperature data used for these calculations came from Entry Island since these have been shown to have a strong positive correlation with average temperatures taken over the Magdalen Shallows on cruises during various times of the year. Since the entire temperature cycle is known for Entry Island and there is a good correlation between Entry Island temperatures and those on the Magdalen Shallows, the temperature at which peak spawning occurs in any given year can be determined. The difference in days between the data of this peak spawning temperature and the midpoint of the cruise is interpreted as the number of days before or after peak spawning. The number of stage 1 eggs is then estimated for the peak spawning date. Now, if the mean and standard deviations of the spawning cycle are known, and the day and the abundance of eggs occurring on that day as it relates to the spawning are known, then the total number of eggs spawned during the spawning cycle can be calculated.

The estimated total number of eggs can now be used to make an estimate of the size of the spawning stock. Data are available on the maturity-at-length, fecundity, and population structure. MacKay (1976) has stated that maturity for mackerel does not shift with length, therefore calculation of maturity-at-age from year to year can easily be made.

MacKay (1976) found that mackerel fecundity (E) can be related to gonad weight (GW) by the following relationship:

$$E = 4451 \times GW \qquad (1)$$

Gonad weights have been taken during regular commercial sampling since 1973. These gonad weights are smoothed over ages by fitting a von Bertalanffy curve for particular years. Fecundity estimated in this manner agreed well with Sette's (1943) estimate. MacKay (1976) has stated that mackerel spawning in the Gulf of St. Lawrence are not batch spawners even if ovary examination during spawning time reveals four oocyte size groups. Ware's (pers. comm.) observations also agree with those of MacKay, indicating, furthermore, that all three larger size groups will be shed during the current spawning season. This fact in conjunction with the short spawning cycle would indicate that mackerel are not batch spawning.

Very few, if any, 1-yr-old mackerel spawn. Therefore, the maturity ogive was applied only to 2+ fish. The population structure was taken from Anderson and Paciorkowski's (1978) latest assessment of the northwest Atlantic mackerel stock. The numbers-at-age of the spawning stock can be calculated from the formula

$$N_{2-10} = \sum_{i=2}^{i=10} \frac{P_i \times M_i}{\sum_{i=2}^{i=10} P_i \times M_i \times E_i} \times E_{tot} \qquad (2)$$

where N_{2-10} is the number of females between age 2 and 10, Pi is the percentage of age group i in the population, M is the maturity at age i, E_{tot} is the egg production calculated from the surveys, and E is the fecundity at age i. The total stock is found by multiplying by 2 assuming a 1:1 sex ratio. By dividing through by the proportion mature at age, immature fish can also be included.

The results of these calculations appear in Tables 1 and 2 with the associated fishing mortality values. Based upon these calculations it would seem that there are more mackerel in the Gulf of St. Lawrence than Anderson and Paciorkowski's (1978) assessment for the entire eastern seaboard of North America.

THE BASIC ASSESSMENT DATA FOR COD

Catch-at-age

Basic data collected between 1960 and 1970 have previously been discussed by Halliday (1972) and are summarized briefly here. The commercial sampling information has been broken up into the following categories: otter-trawl landings in the period January to April in the 4V fishery and otter-trawl, Danish and Scottish seine, line and gillnet landings in May-August as one period and September-December as another period, in the 4T component of the fishery. Biological sampling for the length and age composition of the landings in these categories in the 1960-77 period are fairly complete for the southern Gulf of St. Lawrence (4T) fishery. It was considered more appropriate to treat the winter fishery in Sydney Bight (4Vn) separately despite poor sampling by all countries. However, coverage of this fishery has vastly improved, especially since it is now largely Canadian. Danish and Scottish seine landings were treated separately when samples from them were available, but otherwise were combined with otter-trawl landings. While the age composition of the catch by Danish seines usually shows full recruitment of fish 1 yr younger than by trawls, they have formed such a small part of the total catch that the error produced by combining them with the trawl landings is small. In the last few years this is not the case, since Danish seines have become an important component of the fishery and therefore have been weighted into the overall sample separately.

Gillnet and line landings could not be simply added to the trawl landings since the selection patterns are dramatically different (Fig. 6). When there were no length-frequency samples from line or gillnet landings in a particular year, those of the preceding and subsequent years were combined. Some 1971 samples were applied in this way to the three immediately preceding years. Since 1970, the sampling of all fisheries has been thorough and no interpolating from other years was necessary.

Catch-at-age data between 1950 and 1960 should be regarded cautiously since sampling information is available for only the winter trawl fishery for the entire period (Paloheimo and Kohler 1968). Long- and handlines and some gillnets made up a substantial proportion of the fishery during this period in addition to an inshore otter-trawl fleet of small vessels. In years when samples were available for these gear types they were weighted into the overall catch-at-age frequency accordingly, but in years when samples were lacking an average catch-at-age frequency for that gear type was used. Substantial amounts of fish were discarded at sea (which was practiced) from 1950 until mesh regulations were

strictly enforced in 1959, especially of 3- and 4-yr-old fish (Paloheimo and Kohler 1968). No annual study was conducted during this period so that discards could not be directly accounted for; however, a discard study was carried out from 1949-56 so that the degree of error in the other years can be estimated. By running cohort analysis with and without the average discard for ages 3-5 during the period 1950-60 applied, it was found that the estimate of numbers at age 3 varied by no more than 10%. Catch-at-age data, not including the discards, are presented in Table 3.

Fishing effort

The previous discussion indicates that the Gulf of St. Lawrence cod fishery is rather diverse. The only gear type for which effort data are consistently available is the 26-50 ton otter-trawl fleet. Therefore, this gear type has been used as the standard for the period. One aspect that detracts from its usefulness upon first inspection is that it currently accounts for only 5% of the total catch, compared with 75% in the early fifties. However, the correlation between the catch-per-unit-effort of 26-50 and 51-100 ton vessels from 1962 to the present is very good, suggesting that the catch rate by the smaller vessels still reflects the catch rates in the overall fishery.

The efficiency and fishing power of the Gulf of St. Lawrence fleet most certainly have changed since the otter-trawl fishery first began in 1947. The progressive buildup of larger trawlers and the decline in prominence of the gillnet and longline fisheries are only two of these changes. To analyse a change in gear efficiency, a trend was sought between fishing mortality per unit effort (FUE) and time. The fishing mortality values were those generated by virtual population analysis. It was noted the FUE increased exponentially with time suggesting that efficiency was increasing at a constant instantaneous rate. A relationship of this sort had previously been hypothesized (Halliday and Doubleday 1976) for the Scotian Shelf stocks in general.

The relationship for analysis was

$$FUE = \beta_0 \exp \beta_1 \Delta t$$

where β_0 is a fitted constant, β_1 is the instantaneous increase in efficiency, and Δt is the number of years since 1950.

The reduction in the total sums of squares after fitting the mean due to the exponential of Δt was 39%, the value β_1 was equal to 0.0313, suggesting that efficiency for this fishery was increasing at a rate of 3% per year since at least 1959 when mesh sizes were enforced. Effort values were accordingly adjusted by multiplying them by exp Δt with 1950 being considered year zero.

In 1976 and subsequently the southern Gulf of St. Lawrence was closed to fishing by vessels longer than 100 ft. In addition, the number of large vessels fishing in 4Vn was substantially reduced. This probably ended the continual gain in efficiency and, with the virtual closing of the 4Vn fishery in 1977, the efficiency is probably equivalent to that in the early sixties. To calculate the effective effort (f_F) in any given year, the following formula is used:

$$f_F = \frac{C_T}{c_s} \times f_s \times \exp\ 0.0313\ \Delta t \qquad (3)$$

where C_T is the total catch, c_s is the catch by 26-50 ton trawlers, and f_s is the fishing effort of 26-50 ton trawlers.

Because of the diverse nature of this fishery and its constant change, a valid sequential population analysis cannot be performed until something is known about selection, so that proper starting fishing mortality (F_T) values can be determined. Since 1957 the $4\frac{1}{2}$-in. (11.4-cm) otter-trawl mesh standard has been in force. Selection experiments were carried out only on otter trawls. The selection ogive was the cumulative distribution function of a normally distributed random variate (Fig. 6) with mean 40 cm and standard deviation 7.5 cm derived from the data in Holden (1970):

$$\vartheta_a = \frac{1}{7.5\sqrt{2\pi_0}} \exp\ [-(X-40) \times 7.5]^2 dx \qquad (4)$$

For longline, handline, and gillnet selection it was necessary to turn to the commercial catch sampling data. The strong 1959 year-class was chosen to follow through between ages 4 and 14 so that year-class effects would not confound the analysis. The fraction of the total catch from commercial catch sampling data attributable to each 3-cm length class was accumulated over the years between 1960 and 1974 as the year-class grew and passed through the fishery. These accumulated fractions gave a selection curve but were confounded with the effects of the abundance at given lengths.

To remove the effect of varying abundance a relationship was explored between the cohort numbers-at-age and the average length of the cohort as it grew older. A predictive equation was developed and abundance levels for each 3-cm length grouping were estimated. By dividing these estimates into the accumulated percentages a more unbiased estimate of selection could be determined. Polynomials were fitted to these relationships of the form

$$\vartheta_a = \beta_0 \exp\ (\beta_1 L_a - \beta_2 L_a^2) \qquad (5)$$

which adequately fits a normal distribution where L is the length of cod and β_0, β_1, and β_2 are fitted constants, and the maximum of the curve was given as selection of one (Fig. 6). However, by using this method it is impossible to remove the effects of availability.

Selection in the otter-trawl fishery begins at approximately 22 cm while longline and gillnet selection begin at 31 and 49 cm respectively; full selection occurs at 61 cm in the otter-trawl fishery, 72 cm in the longline and handline, and 86 cm in the gillnet fishery (Fig. 6). Danish-seine selection is assumed to be the same as otter-trawl selection. It is rather peculiar that the selection in the longline and handline fishery falls away so symmetrically at the upper end; however, this response has been noted for other line fisheries. It seems that the bait is unsuitable for large cod and that the hook size may become inefficient. It is doubtful that large cod are merely not as available to the gear since the division between size groups of fish seems to be more related to maturity. Furthermore, research surveys indicate

that cod over 73 cm are just as available as smaller cod in areas of longline fishing.

The three selection curves were combined such that an overall selection for each year since 1960 could be determined for the fishery. Weighting factors, based on the catch-at-age, were calculated for each age group and combined in accordance with the overall catch in numbers of that age group within the gear type, the mean length of the age group dictating the selection. The results of these calculations are shown in Table 5.

Sequential population analysis

The sequential population method used was cohort analysis (Pope 1972) to determine the numbers-at-age from the catch-at-age information (Table 3). Starting values were determined by using an iterative process. First a guess was made for starting F_T values in 1975 and this was distributed over age according to the selection factors (Table 5) in that year. The starting F for the terminal ages in the different years was 0.2. Natural mortality (M) was held constant at 0.2 for all age groups (Halliday 1972). A study using Paloheimo's (1958) method agreed with Halliday's conclusion for ages 3-14 when the CUE was divided by the selection factors. However, this is not to say natural mortality does not vary with age; it is merely applied as an average value.

Estimates from cohort analysis improve as F values accumulate; thus after the initial run the average F was determined for fully recruited age classes and F values for the oldest age groups were determined by multiplying these average F's by the appropriate selection factors. The F value in 1975 was determined from a plot of fishing mortality versus effective effort. The analysis was again run, and the same procedure was followed with the exception being that the average F for ages 3-15 was now regressed against effective effort and a value for F in 1975 was predicted. This value when re-run gave the relationship in Fig. 7. Since no selection factors were available prior to 1960, an average F of 0.28 was used for the oldest age groups (Table 2).

The correlation between average F_{3-15} and effective effort is quite good and does indicate that management of fishing effort can have substantial impact on the resultant mortality rates within the cod stock (Fig. 7). The lack of trends in the residuals indicates that errors occur randomly and that there are no between-year effects in natural mortality. When the F value for each age group is correlated with the age-specific selection times effort values, there was a correlation between the residual value and age which might be attributed to age-specific natural mortality. Numbers-at-age and F values are shown in Tables 6 and 7.

Research survey data

Although Fig. 7 indicates a good correlation between F and effective effort, it does not give an exact estimate of the present levels of fishing mortality due to the scatter of the relationship. Therefore, it is necessary to look at an independent data source to check on these values.

Research surveys have been conducted in the Gulf of St. Lawrence since 1959. These began as fixed stations in the Chaleur Bay area. An average of 28 stations were covered between 1959 and 1969. In 1970 a preliminary random stratified survey was made and by 1971 a full random stratified survey was installed.

The objective of this type of survey was to have more than one station in a particular stratum so that some estimates of the error mean square could be made. The stratification was based upon depth since this was the one factor that seemed to apply to the distribution of most species. Furthermore, depth, bottom type, and temperature all seem to be correlated with one another.

The stratification by depth does reduce the variance in catch due to different fish species but does little to reduce the variance within species. A preliminary appraisal of stratification by depth for cod would indicate that it is no better and perhaps worse than fixed stations.

Since the setting up of the stratified random survey, 12 of the fixed stations around Chaleur Bay have been retained where abundance levels are highest (Fig. 1). To check on the abundance levels from cohort analysis, the numbers of 3+ fish from cohort analysis in year t + 1 were plotted against the catch-per-unit-effort of 2+ fish from the Gulf surveys in year t (Fig. 8). Only the catch-per-unit-effort from fixed stations was used. The reason for the 1-yr lag is that the standard Gulf cruise occurs in October when the fishery is almost over and the aging convention is a January 1 birthdate for numbers-at-age.

The CUEs from the Gulf surveys are variable from year to year. Therefore, these numbers are smoothed by using a 3-yr running average since it is really the average of 2-, 3-, and 4-yr-olds that makes up the bulk of the survey index. The total estimate from virtual population analysis correlates very well with catches from the survey (Fig. 8), especially since the data are not a time series (Table 8). However, this relationship does not go through the origin indicating that 1×10^8 cod are not sampled each year, although it is unlikely that this is a plausible explanation.

One suggestion might be that natural mortality has been underestimated for cod, and a higher value would put regression of these two variables through the origin. An M of 0.3 increases the population size in the early and mid-sixties and decreases the population size in the mid-seventies (Fig. 8). Since later years are associated with lower CUEs, the effect is to increase the slope of the relationship. However, this manipulation substantially increases the scatter of the relationship. Furthermore, no cod population in the world has been found to have an M value this high, and the calculation of natural mortality, using Paloheimo's method for this stock, does not support the hypothesis of an M higher than 0.2. Indeed, Paloheimo and Kohler (1968) calculate M to be 0.19 for southern Gulf of St. Lawrence cod; Halliday (1972) upon a re-analysis of their data reaches a similar conclusion.

Another explanation could be that the catchability, through availability, is related to stock size. This phenomenon has been shown to be true for a variety of pelagic fish stocks (Cushing, pers. comm.). It is quite possible that the catchability of cod increases with stock size since these fish have certain seasonal feeding grounds where concentrations can be found. Fishermen know where these concentrations are, and have fished in these areas for decades. Therefore, the fraction of the local

populations removed by a unit of effort would increase as the population decreased and vice versa.

Consider the following formulation: If the catchability coefficient, q, increases with population size, P, then

$$q = \beta_0 P^{\gamma} \qquad (6)$$

where β_0 is a constant and $(1 < \gamma < 1)$.

The normal assumption (Ricker 1975) is that fishing mortality, F, is linearly related to effort, E,

$$F = qE \qquad (7)$$

Rearranging the catch equation (Beverton and Holt 1957) gives,

$$C/F = P\left[\frac{1 - \exp(-Z)}{F + M}\right] \qquad (8)$$

where Z is the total instantaneous mortality rate. By combining equations 6, 7, and 8 and rearranging terms the following equation can be formulated:

$$C/E = \beta_1 P^{\gamma+1} \qquad (9)$$

This formula assumes that fishing effort is not changing from year to year, which is true for a standard groundfish survey. Equation 9 can be rearranged to correspond with the functional relationship in Fig. 8,

$$P = \beta_2 (C/E)^{\frac{1}{\gamma+1}} \qquad (10)$$

where β_2 would be a fitted constant.

As long as $(\gamma+1) > 1$, then the estimated population size should appear to depart from linearity as a power function of the CUE. Therefore, in the case of the Gulf of St. Lawrence cod stock, if the relationship between CUE and the 3+ numbers from cohort analysis is assumed to be linear, it could result in overestimates of stock size at higher and lower CUEs.

If equation 10 were fitted to the data, the relationship would go through the origin. The above explanation probably best describes the incongruity of Fig. 8.

Using the smoothed CUE value for 1977 gives a predicted number-at-age in 1978 of approximately 2.6×10^8 3+ cod. The catch projection from 1977, using the catches generated in that year, gives a total of 1.6×10^8 4+ cod in 1978. Thus by subtraction the estimated 1975 year-class size is 1.1×10^8 in 1978.

Juvenile surveys and prediction of year-class size

Previously a correlation was found by Hare and Kohler (1974) between the CUE of juveniles and year-class size as estimated from virtual population analysis. Since the juvenile surveys in former years did not cover the entire Gulf of St. Lawrence, and were conducted with different mesh and vessel sizes, the two surveys were intercalibrated in 1971-73. In these years the correlation between the catch per tow of the old and new surveys was almost perfect. The values from the old surveys between 1957 and 1970 were corrected to be equivalent to the new random stratified surveys (Table 9).

The correlation between the numbers at age 3 from VPA and the catch of age 2 cod of the same year-class from the juvenile surveys was indeed high ($r = 0.90$). The equation for the Geometric Mean (GM) regression (Ricker 1973) was as follows:

$$N_2 = 6081.58\ CUE_2 + 226687 \qquad (11)$$

Because cod are distributed in groups and there is a segregation of small cod from larger cod, it is quite possible to overestimate the CUE for young cod when they are abundant. The survey has not been stratified, or randomized for the distribution of different age classes of cod. The young cod were concentrated mainly in Miramichi Bay and spread out from there in diminishing numbers.

BIOLOGICAL DATA RELATING TO GROWTH AND MATURITY

Density-dependent growth for cod

The instantaneous growth rate,

$$G = \frac{dW}{dtW},$$

can be calculated by the natural logarithm of the ratio of weights (Q) in successive years (Ricker 1975). These rates were calculated for cod ages 2-15 from weight-at-age data from commercial sampling between 1950 and 1977 (Table 10). These samples were taken between January and April when the cod change weight very little (see Fig. 10).

Lett et al. (1975a) have previously shown that the growth rate of cod between ages 5 and 8 in the Gulf of St. Lawrence is inversely related to the population biomass, and that the biomass reflects the density of the stock. However, as this is an average rate it is difficult to apply to the overall stock. Since the instantaneous growth of fish is an inverse power function of the weight, the relationship between these two variables can be linearized by a double logarithmic transformation. Therefore, density and weight are considered to be the two variables most affecting the growth of cod when the total carrying capacity of the Gulf of St. Lawrence system for cod remains relatively unchanged.

However, the accumulated effects of the epizootic disease (Sindermann 1958) in the Gulf of St. Lawrence did lead to some substantial changes in the growth rate of cod between 1950 and 1956. During this period the biomass of mackerel and herring was reduced to a very low level. The disease which started gradually and caused catastrophic mortalities near its termination may have been related to higher than average water temperatures which prevailed during this time. The increase in the growth of cod was partially related to the ease of capture of diseased prey (Kohler 1964). Furthermore, because of the removal of a major portion of the pelagic fish community, more energy could have been transferred directly into the benthos, which would increase the carrying capacity for the benthos, and the availability of food items for young and old cod alike. This situation in the Gulf of St. Lawrence is similar to that noted in the North Sea where the pelagic biomass is now at a low level because of overexploitation, but substantial increases have been noted in the cod biomass. Jones (1976) has presented a preliminary investigation of possible energy flows in the North Sea system which

elucidates the partitioning of energy in an attempt to explain the observed changes. The following equation represents cod growth:

$$\frac{dW}{dtW} = \beta_0 \times B^{-\gamma_1} \times W^{-\gamma_2 \ln B} \quad (12)$$

where the biomass (B) in metric tons is that existing after the 4Vn fishery is completed and W is the weight of cod in kilograms. It is not clear why B fits the data best as a logarithm in the exponential. However, equation 12, as other equations presented in this paper, is partially based upon biological theory and partly empirical.

The collective effects of the epizootic disease between 1950 and 1956 on cod growth will be represented as a dummy variable (D), as described in Draper and Smith (1966). The dummy variable is zero when the disease is not occurring and one when it is. The following equation fitted by using stepwise multiple regression minimized the error mean square:

$$\ln G = \gamma_1 \ln B + \gamma_2 \ln B \times \ln W + (\gamma_3 \ln W) \times D + \beta \quad (13)$$

Parameter	Value	Standard error
γ_1	-0.2515	0.0922
γ_2	-0.0517	0.0050
γ_3	0.1471	0.0803
β	1.8869	

The coefficient of multiple determination (R^2) is 0.47 while F (significant at P > 0.5) for regression is 65.32 ($F'_{3,221}/2.60$).

A significant interaction between weight and the dummy variable indicates that when the epizootic is not occurring weight is more influential on growth rate. This suggests that the epizootic in fact increased the energy intake of cod. Since the epizootic is not a 'normal' event, equation 13 would be the most useful for management of cod. As the weight of cod increases the instantaneous growth rate declines rapidly (Fig. 9) with the growth rate of smaller fish being more affected than that of older fish by shifts in biomass. This would make density-dependent growth in most fish stocks extremely hard to detect.

Seasonal growth of cod

The seasonal growth pattern for cod is difficult to determine from field data due to a combination of sampling errors and economics. Therefore, monthly growth rates were determined by Waiwood (unpubl.) for laboratory held fish at different temperatures and fed varying rations. It was found that growth rate correlated with appetite extremely well. This was evident in a seasonal pattern (Fig. 10) which was calculated by knowing the average monthly temperatures in the Gulf of St. Lawrence.

The growth rate for adults declines during the early part of the year and actually becomes negative in April and May prior to spawning. However, during the same period juvenile cod would not lose weight. Maximum growth rate is in October and declines through November and December. By using the relationship described by Fig. 10 and knowing the annual growth rate, incremental growth rates, for example, on a monthly basis, can be calculated to simulate a seasonal pattern in the fishery.

Growth changes in mackerel

Length-at-age between 1962 and 1976 was determined from Canadian 4X catch statistics and data from MacKay (1976). In years when MacKay's data and the Canadian Div. 4X sampling data overlapped the average lengths-at-age were determined by using weights in accordance with sample sizes. The data for the years between 1965 and 1977 are presented in Table 11. The Div. 4X samples were used since they gave the only consistent set of data over the entire period. Length-weight relationships in individual years were available from MacKay (pers. comm.) and from the Canadian 4X sampling. These relationships were used to convert length to weight (Tables 11 and 12). No sampling was carried out in 1972 and the values were interpolated by using a Walford plot; however, with this method it is impossible to get lengths for fish in the first year, since the relationship becomes nonlinear for the youngest age groups. The 1973 data were questionable, the problem probably due to experimental error attributable to change in personnel.

Density-dependent growth has been noted for a number of fish stocks other than 4T cod but usually not very clearly. In fact, the concept of density-dependent growth is viewed as dubious by some (Cushing and Horwood 1976). Varying growth rates following maturity are usually difficult to determine, especially for a fast-growing fish like mackerel, since it may be ecologically advantageous for fish to remain on a particular growth schedule that coincides with available particle sizes of food items, at different stages. When an optimal adult size is reached, surplus energy is then diverted to gonad production. This is especially true for schooling fish (Ware 1975a) such as herring and mackerel where an optimal foraging size is extremely important. Therefore, it was not unexpected that density-dependent growth was detected for Gulf of St. Lawrence cod but not herring (Lett and Kohler 1976).

The growth rate of mackerel varies widely on an annual basis but no correlation could be found between the instantaneous growth rate of mackerel and the stock biomass. Temperature was found to be significant in explaining variations in the growth of mackerel, but these were summer temperatures in the Gulf of St. Lawrence which would only describe a portion of their seasonal growth.

Winters (1976) shows a negative correlation between mean size of certain age groups in given years and herring biomass but the sizes of the herring do not give any information on growth in individual years. Although he assumed that he demonstrated density-dependent growth, he in fact, did not.

Density-dependent growth of cod and mackerel in the first year

The occurrence of density-dependent growth during the first year of life in the Gulf of St. Lawrence cod stock was investigated by using the back calculation of 2500 otoliths taken from commercial sample surveys for the years 1960-75. When measurements from the focus to part of the

annulus are made, the measurement referring to growth in the first year is called the ℓ_1 growth. For each year, 150 otoliths covering all available age groups were read according to the methods of Kohler (1964) and May (1965). The interface between the outside edge of the opaque band and the inside edge of the hyaline zone was taken to be an annulus. The resulting regression between fish length (L, in cm) and otolith radius (R_0, in mm) was found to be:

$$L = 0.628\ R_0\ 1.227 \qquad (14)$$

The coefficient of determination (r^2) was 0.73. According to age and year of capture, the otolith measurements for each fish were sorted into year-classes. The sample sizes ranged from 32 for the 1950 year-class to 183 for the 1964 and 27 for the 1972 year-class. The mean growth in centimeters for each year was calculated for each age class.

Density-dependent ℓ_1 growth has been shown to exist for clupeids (Marr 1960; Iles 1967; Lett and Kohler 1976) and for gadoids (Raitt 1939; Doubleday et al. 1976). However, although the relationship is observed, it is difficult to conceive of a biological theory that would adequately explain all the events that could occur in the first year. For cod, it was assumed that temperature (T_P) in the Bay of Chaleur region would affect growth in the first year. Furthermore, in other examples of density-dependent ℓ_1 growth, the relationship between length and density is not linear. For cod the density was taken to be the abundance at age 3 since there are no measures of numbers younger than this. As mentioned previously, the epizootic disease probably had a substantial effect on both the growth of juvenile and adult cod. As above, a dummy variable (D) was used to represent the presence or absence of the epizootic. The curve that was fitted by multiple regression has virtually no biological basis, but simply is a rationalized, empirical representation of the data.

The following equation, of several tried, describes much of the variation in early growth of Gulf of St. Lawrence cod:

$$\ln \ell_1 = \gamma_1 \ln N_3 + (\gamma_2 \ln N_3) \times D + \gamma_3 D + \gamma_4 \ln N_3 \times \ln T_P + \beta \qquad (15)$$

Parameter	Value	Standard error
γ_1	-0.2999	0.0459
γ_2	0.2725	0.0931
γ_3	-2.9395	1.0486
γ_4	0.02202	1.0486
β	4.7157	

The coefficient of multiple determination (R^2) was 0.71 while F (significant at $P < 0.05$) for regression is 10.79 ($F'_{4,18}/2.29$).

As year-class size increases, there is an exponential decline in ℓ_1 length. The shape of this relationship agrees well with the exponential decline in ℓ_1 length for silver hake in response to year-class size noted by Doubleday et al. (1976).

A more useful form of the equation in the absence of an epizootic is (Fig. 13):

$$\ell_1 = 111.69\ N_3\ (0.02202 \ln T_P - 0.2999). \qquad (16)$$

The yearly fluctuations in the first year of cod growth are most interesting. The variations cannot be explained by larger, faster growing fish dying sooner (known as Lee's phenomenon), or by an increase in experimental error due to lower sample sizes in most recent years. In addition to density-dependent first year growth, there is a suggestion of growth compensation in the second and third years, where first year growth was low, second year growth was usually high, and vice versa.

For mackerel the first year's lengths were those measured in the commercial sampling of the 4X fishery and the 0-group year-class size came from sequential population analysis (Fig. 11). No values were available for 1971 and 1972 year-classes for the reasons mentioned previously. The relationship seemed to be almost linear, but as with cod a non-linear function gave the best fit:

$$\ell_0 = 279.94 \exp(-2.531 \times 10^{-5}\ N_0) \quad r^2 = 0.73 \qquad (17)$$

where N_0 is the number of 0-group fish and ℓ_0 is the length in the first year from 4X sampling. Temperature was also tested for significant correlations with growth but no relationship was found as was the case for cod. However, it is probable that mackerel, being highly mobile, are much more stenothermal than cod; therefore fluctuations in temperature probably affect their growth rate less since they can avoid them. Indeed, temperature is probably the controlling factor which causes the fall migration of 0-group mackerel from the Gulf of St. Lawrence.

Shifts in maturity with length

Recent work by Daan (1974) and deVeen (1976) indicate that maturity as a function of length is a dynamic trait of cod and sole. Shifts in length at maturity can have an extreme impact on the total egg production of the population; thus it would seem that such a characteristic as this one should have some biological significance although its physiological basis is not clear. Length at maturity dropped 13 cm between 1959 and 1974 for Gulf cod (Fig. 12).

Beverton and Holt (1959) noted that maturity usually occurs at the inflection in the relationship of weight on age.

A PRELIMINARY ANALYSIS OF THE BIOENERGETICS OF THE RECRUITMENT PROCESS

EGG PRODUCTION BY THE ADULT STOCK

Although many published studies assume that fecundity is fixed in relation to length, some studies involving the feeding of fish in laboratories indicate otherwise (Scott 1962; de Vlaming 1971; Tyler and Dunn 1976; Smith et al. 1978; Waiwood 1978). Furthermore, there have been a number of field studies which indicate that the slope of the fecundity length relationship changes from year to year (Bagenal 1973; deVeen 1976) with the proposed mechanism usually being a change in ration size. Recently, Waiwood (1978) has shown in laboratory experiments conducted at different temperatures and ration sizes that gonad weight and fecundity are related to the change in weight of cod 6 mo after spawning in the previous year. The mechanism for this effect in cod had already been theorized by Woodhead and Woodhead (1965). Apparently, there are three growth stages of cod eggs. The smallest oocytes will not mature in the coming reproductive period and the largest will

always mature but may not be spawned. The intermediate group may be brought to maturity depending upon the amount of 'surplus' energy available. This is possibly the reason why Hislop and Jones (pers. comm.) notice a tenfold increase in egg production with a doubling in the ration size fed to haddock. Mathematically the general relationship can be represented by the equation:

$$E \propto N \times (\Delta\hat{W})^{\gamma} \qquad (18)$$

where E is the egg catch in the Gulf of St. Lawrence surveys per 1 000 000 m^3 of water, N is the number of mature fish, and $\Delta\hat{W}$ in kilograms per year is the weighted growth rate of the mature stock. The exponent, γ, determines the rate at which surplus energy is being channelled to gonad in relation to the overall surplus energy represented by a change in weight.

Lett et al. (1975a) have shown that temperature (T_p) influences the survival and catches of eggs on ichthyoplankton cruises. In addition, it had been shown that temperature acts nonlinearly. A quadratic expression has been used by Forrester and Alderdice (1966) for Pacific cod and Bonnet (1939) for Atlantic cod. Therefore, the following equation was fitted to represent the catch of eggs during the time of peak spawning:

$$\ln [E/N] = \beta_1 \ln \Delta\hat{W} + \beta_2 T_p + \beta_3 T_p^2 + \beta_0 \qquad (19)$$

Parameter	Value	Standard error
β_1	1.2221	0.3640
β_2	1.6769	1.1114
β_3	-0.1655	0.1071
β_0	1.780	

The reduction in the total sums of squares, due to regression, was 77.3%, with an $F = 6.8$ ($F'_{3,6}/4.76$). The equation can be rearranged to the following form:

$$E = 5.93 \times \exp (1.677\ T_p - 0.166\ T_p^2) \times N\ (\Delta\hat{W})^{1.222} \qquad (20)$$

where T_p is the mean sea surface temperature occurring on the cruise. Although neither β_2 nor β_3 is significant the combined effects of the fitting of these two parameters led to an improvement in the overall fit by 9%. Most of the variation (69%) in egg catch per mature individual is explained by the growth rate, which is a measure of production of surplus energy by individual fish (Fig. 14).

For a stock where $\Delta\hat{W}$ did not change there is, as often assumed, a linear relationship between biomass and egg production, but this has limited biological meaning. Lett et al. (1975a) and Lett and Doubleday (1976) presented a dome-shaped egg-production curve as a function of biomass for the Gulf cod and hypothesized at that time that density-dependent growth led to the production of this dome-shaped curve. Equation 20 certainly supports this conclusion since, according to equation 12, $\Delta\hat{W}$ should decrease as N increases and the rate at which egg production declines with density depends on the exponent of $\Delta\hat{W}$.

MacKay (1976) has shown for the northwestern Atlantic mackerel stock that gonad weight is a power function of fork length with the exponent being greater than one. Furthermore, he showed that the exponent of this relationship in different years is positively correlated with the annual growth rate of the stock. A similar relationship has been shown for the Pacific horse mackerel. For this reason it is hypothesized that the general mechanism by which mackerel produce eggs is similar to that of cod. To study this it was necessary to determine an index of mackerel egg production in the Gulf of St. Lawrence.

Mackerel are very sensitive to changes in temperature (Sette 1950). This is important when interpreting the egg data. During peak spawning 60-80% of the variation in the relationships described by the logarithm of egg abundance between stations is explained by temperature. The response is dome-shaped, adequately described by a quadratic temperature term. There are usually two or three areas in the Gulf where egg concentrations are exceedingly high, with catches reaching 1.8×10^6 eggs per half-hour tow, although eggs are caught at all stations, even those where temperatures are low (8°C). The biological basis of this phenomenon can be explained by mackerel searching for an optimal spawning temperature. Statistically the effect is easily removed through an analysis of covariance.

At similar temperatures the catches of eggs are not normally distributed, with low catches predominating over high catches. For this reason the logarithm of egg abundance was used in the analysis of covariance, temperature being the covariate. This analysis substantially decreased the variance of the geometric mean egg abundance.

The spawning period of mackerel in the Gulf of St. Lawrence follows a normal distribution in time in relation to temperature for the reasons already discussed. The duration of spawning is well defined, beginning in mid-June and ending in late July; however, when more eggs are deposited the cycle is slightly more protracted. The magnitude of the mode of egg production can vary greatly from year to year depending on the biological state of the stock.

During 1966 to 1969 at least five cruises occurred yearly, and of these at least four caught mackerel eggs in the surface meter nets. A curve was fitted to these egg counts using the model

$$E = \beta_0 \exp (\beta_1 T_p - \beta_2 T_p^2) \qquad (21)$$

where E is the catch of eggs per 1 000 000 m^3 of water strained, and T_p is surface water temperature (°C) on the cruise. It is assumed that regression residual values resulted from variation in annual production of the adult stock. The temperature of maximum egg production was estimated at 12°C by solving for the first derivative of the logarithm of egg catch. Although all cruises occurred during peak spawning, the duration of the cruise would put the geometric mean value slightly on the left- or the right-hand side of the actual peak. Thus the logarithm of egg abundance could be corrected to a value corresponding with that of the optimal temperature. This peak value then is an index of the overall egg production, or the area under the production curves, since the duration of spawning varies little from year to year.

Year	Natural logarithm Peak abundance per 1 000 000 m^3 in the Gulf of St. Lawrence, ±1 (SE)
1967	11.18 ± 0.842
1969	12.41 ± 0.490
1976	13.94 ± 0.148

The Gulf of St. Lawrence survey was extended onto the Scotian Shelf in 1977 to see if spawning occurred there at the time of peak spawning in the Gulf of St. Lawrence. No mackerel eggs were found, but in 1976 an August survey on the Scotian Shelf caught mackerel larvae. However, these catches were so small compared to those in the Gulf, the major spawning of the northern contingent of the mackerel stock was assumed to occur in the Gulf of St. Lawrence.

As for cod, equation 20 should describe the production of eggs by mackerel. However, contrary to the relationship formulated for cod the catch of mackerel eggs should not be contingent on temperature (equation 22) for two reasons: First, mackerel select a temperature near 12°C to spawn and the eggs are spawned pelagically near the surface while cod eggs are spawned benthically and float up through the water column into the mixed layer, so temperature could change greatly. The second reason is that mackerel eggs hatch within 4-6 d, while cod eggs require between 20 and 30 d (Worley 1933; Forrester and Alderdice 1966), thus the chance of a substantial change in temperature while mackerel eggs are developing is less likely.

The relationship for mackerel egg density was fitted in a similar manner to that for cod to yield the following equation:

$$E = 6876 \times N (\Delta\hat{W})^{1.579} \quad r = 0.98, 2 \text{ df} \qquad (22)$$

where E is the egg catch per 1 000 000 m^3 of water, N is the number of mature mackerel, and $\Delta\hat{W}$ is the weighted mature mackerel growth rate.

For both mackerel and cod the relationship between egg production and $\Delta\hat{W}$ is similar (Fig. 14, 15). The exponent on the relationship for mackerel is higher than that for cod, but this is to be expected because of the higher metabolic rate of mackerel. Based upon field observation then, it can be suggested that the physiological mechanism by which mackerel produce eggs in response to surplus energy is probably similar to that for cod.

THE PRODUCTION OF LARVAE

The survival of fish larvae has been a topic of particular concern to fisheries biologists for the past century; however, few papers consider the combined effects of environment and density-dependence in a quantitative manner with the exceptions of Ware (1975b), Lett et al. (1975a, b), and Lett and Kohler (1976).

The quantitative model developed for cod in this paper incorporates the two effects. The normal assumption concerning the survival of fish is that

$$\frac{dN}{dt} = \beta_0 N^2 \qquad (23)$$

Ware (1975b) hypothesized that mortality is related to the growth rate, a relationship which seemed well supported by the data. Unfortunately, the data are not yet available on the growth of juvenile and larval cod so in this study it is proposed that the mortality rate responds to density.

The structure of the relationship between density and mortality is not known. A plot of the instantaneous mortality rate versus numbers over the period when larvae are available is an asymptotic relationship with population density. This was one of a number of possible combinations tried:

$$\frac{dN}{dtN} = \beta_1 \ln N + \beta_2 (\ln N) \times T_P^2 + \beta_0 \qquad (24)$$

Parameter	Value	Standard error
β_1	1.639×10^{-2}	2.470×10^{-3}
β_2	-1.751×10^{-5}	1.000×10^{-5}
β_3	-0.0485	

where T_P is the annual monthly maximum temperature. The reduction in the total sums of squares due to regression is 88.7% with an F of 35.3 ($F'_{2,9}/4.26$). The equation implies that if the temperature and number of eggs are known, the number of surviving larvae is predictable. Of all models considered, equation 24 gave the best fit. Since there is no closed form for integration, the equation in the following form must be solved iteratively:

$$dN = 1.639 \times 10^{-2} \log_e N (1 - 1.0683 \times 10^{-3} T_P^2) - 0.0485 \times N_0 \times dt \qquad (25)$$

$N_1 = N_0 = dN$

$N_0 \leftarrow N_1$

where N_0 is the initial number of animals and N_1 is the number remaining after the time interval, dt. The solutions of the equation are extremely stable when the time interval is 1 d. The number of larvae is estimated after 50 d and the results are the same as in preliminary analysis (Lett et al. 1975a).

Large variations in egg production thus may be compensated by density-dependent larval mortality. Harding and Talbot (1973) present a number of survivorship curves for plaice which indicate a similar response; that is, the number of surviving larvae is much less variable than the number of eggs.

The simulated relationship between the numbers of cod eggs at peak spawning and larvae 50 d later is shown in Fig. 16, when temperature is varied. It suggests that at higher egg numbers the effect of temperature is more influential in determining the absolute numbers of larvae.

Mackerel larvae were caught in large numbers on only two of the Gulf of St. Lawrence cruises; thus it is difficult to specifically discuss their dynamics. However, Arnold (1970) found them to be cannibalistic. This fact has also been noted in tank experiments by Hunter and Sanchez (unpubl.). Furthermore, it is their contention that density-dependent cannibalism is important in the recruitment of mackerel. When mackerel reach about 8 mm cannibalism begins, and ends when they reach 15 mm or metamorphosis. Temperature significantly modifies the growth rate of mackerel larvae (Hunter and Sanchez, unpubl.) and the faster they can reach 15 mm the greater the survival.

FACTORS AFFECTING YEAR-CLASS SIZE

Lett and Kohler (1976) concluded that there was a relationship between larval abundance of herring and year-class size only when larval abundance was low. Indeed, the relationship for a constant level of cannibalism is asymptotic. If the degree of cannibalism varies then no relationship between larval production and year-class size is visible. This must mean then that cannibalism at higher larval abundances is more important in determining year-class size. Indeed, if Lett and Kohler (1976) had not included variables other than abundance of larvae, their conclusion would have been the same as that of Beverton and Holt (1957), suggesting a mean recruitment value with a certain deviation above a critically low stock size.

A previous attempt to derive an equation describing the formation of year-classes from larval abundance has incorporated the effects of predation of older cod on juvenile cod as they become demersal (Lett et al. 1975a). However, this equation failed to predict year-class sizes outside the data surface used to fit the relationship. The equation would not describe the extremely large cohorts in the 1950's or the exceptionally small ones in the early 1970's. It was the conclusion of Lett and Doubleday (1976) that an important variable was missing from the equation.

It is known that the mackerel consume large amounts of fish larvae and eggs (Grosslein et al. 1978; Kulka and Stobo, unpubl.) on Georges Bank, on the Scotian Shelf and in the Gulf of St. Lawrence (Arnold 1970; MacKay 1976). It is very difficult to identify to species fish larvae that have been partially digested, but Kulka and Stobo do show that mackerel consume significant numbers of gadoid larvae. Lett and Kohler (1976) have already indicated the effect of mackerel consuming herring larvae.

The peak of cod spawning occurs as the mackerel are just beginning to enter the Gulf of St. Lawrence in late May and early June. These cod eggs have just hatched and are available as free-floating yolk-sac larvae when mackerel have completed their spawning cycle. Thus the cod larvae are readily available when mackerel are recovering from spawning and eating most voraciously. Furthermore, mackerel remain in the Gulf for the entire summer, feeding in areas occupied by cod larvae.

Lett et al. (1975a) have already theorized that the upper limit of the cod production system is constrained in relation to the production of pelagic fish. Indeed, in the North Sea there has been a significant increase in recruitment to the demersal stocks with the collapse of the herring stocks and some mackerel stocks. However, the present study considers only the interaction between mackerel and cod, although possibly other pelagic species also have a significant effect on the recruitment of cod.

The relationship between year-class size at age 3 ($N \times 10^3$), 3+ cod biomass ($B_c \times 10^3$ tons), and 2+ mackerel biomass ($B_M \times 10^3$ tons) is represented by the following equation. The cod biomass is the average of the 2 yr when the year-class is 0- and 1-group. This was done since it is during these stages that juvenile cod change from being pelagic to being semipelagic or demersal. As the young cod settle to the bottom they are being eaten by the cod that are already demersal. I have found small cod in the stomachs of larger cod in the Gulf of St. Lawrence. Since there is a good correlation between 2-yr-old cod caught by research surveys and 3-yr-old cod from the cohort analysis, it is assumed that the year-class is formed by the second year (Fig. 17). The abundance of larvae, L_R, 50 d after peak spawning is predicted by equations 22 and 25. Essentially, two approaches were taken in the analysis of the data. A form of the recruitment equation with some biological meaning was hypothesized:

$$N_3 = \beta_0 \times L_R \times \exp(-\beta_1 L_R - \beta_2 B_M^{\gamma_1} + \beta_3 B_c^{\gamma_2}) \quad (26)$$

This is a modified Ricker (1954) model which takes into account predation by mackerel and cannibalism by 3+ cod on the juveniles recruiting into the stock. The relative predatory rates of the two species are γ_1 and γ_2 respectively. The model when fitted by nonlinear least squares gave the following parameter values:

$\beta_0 = 7.695 \times 10$ $\qquad$ $\gamma_1 = 0.521$
$\beta_1 = -8.126 \times 10$ $\qquad$ $\gamma_2 = 0.870$
$\beta_2 = -3.650 \times 10$
$\beta_3 = -3.420 \times 10$

The correlation coefficient $r = 0.85$.

Although the overall fit is significant the equation says little about the significance of individual terms. However, it is important to note that γ_1 is less than one while γ_2 is almost equal to one; that is, the instantaneous rate of mortality due to predation by mackerel does not increase linearly as the biomass of mackerel increases. In other words, mackerel are less effective predators of cod larvae as their biomass increases. Only so many schools of mackerel can be in the vicinity of cod larval patches. At some level of mackerel abundance it is likely that some schools will not encounter cod larvae at all.

For cod the situation is different. The demersal cod biomass will occupy certain areas and not others. As the cod numbers increase then density of cod in these areas will also increase and therefore the instantaneous rate of mortality due to cannibalism should be a linear function of demersal stock size.

If γ_1 and γ_2 are taken as 0.5 and 1.0, the equation can be fitted by using linear regression and certain interactive terms can be investigated. Multiple regression was used to fit the data. The following is the best fit of the series examined:

$$N_3 = \beta_0 \times L_R \times \exp(\beta_1 \times B_c \times B_M^{0.5} + \beta_2 \times L_R + \beta_3 \times B_M^{0.5} \times L_R + \beta_4 \times L_R \times B_c) \quad (27)$$

Parameter	Value	Standard error
β_0	4.220×10^3	
β_1	-1.409×10^{-8}	3.659×10^{-9}
β_2	-5.160×10^{-3}	1.545×10^{-4}
β_3	1.457×10^{-11}	5.312×10^{-12}
β_4	2.584×10^{-9}	9.787×10^{-10}

The coefficient for multiple determination was 0.781 while F for regression is 12.5 and the data are well described (Fig. 18, Table 13).

Although an auto-correlated function was used to fit the data, most of the variation is explained

by the statistical interaction of cod and mackerel which may reflect the competition for the feeding on larval and juvenile cod. The 1964 year-class was not well explained, which was a good year-class for cod along the Atlantic seaboard, and thus information is still missing here (Fig. 18). Furthermore, the equation indicates that as mackerel and/or cod decline, year-class size should improve. Only the data between 1954 and 1972 were used to fit this curve. However, if the 1973, 1974, and 1975 year-classes were also used the equation would have fit much better. Surveys indicate that these year-classes have been increasing in size (see research surveys section) and this has happened as both cod and mackerel have declined. A first estimate indicates that the 1975 year-class is one of the largest on record for this stock, when cod and mackerel predatory biomasses were at a minimum; thus the model seems to be valid so far (Fig. 17). There is only one way to test the model as presented here, and that is to see if its predictions hold up in a quantitative way over time. The initial results from 1973, 1974, and 1975 look promising. For larval abundances greater than approximately 200 larvae per 1 000 000 m^3 of water the relationship between larvae and year-class is very unclear, when cod are allowed to vary (Fig. 19). In fact, it is hard to imagine that a relationship exists between parent stock and recruitment for cod over a wide range of stock sizes. A relationship can only be elucidated as the stock begins to decline, a similar result noted for herring (Lett and Kohler 1976). The important variable in this stock recruitment relationship is the stock in its role not as parents but as predators on young cod when they become demersal. Thus, the chances of a good year-class increase as the stock declines until some critical level is reached.

As stated previously, there was some difficulty involved in analyzing data on the mackerel larvae so the subsequent model does not consider them. For mackerel, as with cod, there seemed to be a density-dependent growth relationship in the first year of life. However, for mackerel this density-dependence seemed to be much stronger, possibly because of the cannibalism mechanism suggested by Hunter and Sanchez (unpubl.) and observed in stomach contents collected by Arnold (1970). Temperature has also been suggested to be an extremely important component of the cannibalism mechanism because of its effect on growth rate.

It is hard to imagine a mechanism of cannibalism of adult mackerel on larvae since the larvae grow quickly to sizes that make them unavailable to adults. Thus we have used the same form of the Ricker (1954) model as we used for cod, but included the effects of temperature:

$$N_0 = \beta_0 \times E_M \times \exp(\beta_1 T + \beta_2 E_M + \beta_3 T \times B_M) \qquad (28)$$

where N_0 is the number of 0-group fish ($\times 10^6$), T is the average June, July, August temperature on the Magdalen Shallows, and E_M is the catch of mackerel eggs per 1 000 000 m^3 of water. The curve was fitted from the following data, with egg production being predicted by equation 22:

Year	Mature growth rate	Mature number $\times 10^{-6}$	Egg(E_M) catch	Entry I. surface water temp.(T_P)	Year-class size $\times 10^{-6}$
1966	0.047	1529	70359	15.7	3914
1967	0.041	1619	72473	16.8	10070
1968	0.057	3007	221834	15.7	3852
1969	0.083	5737	776441	15.4	4451
1970	0.104	7251	1402907	15.9	2318
1971	0.038	6803	267733	15.9	2484
1972	0.076	5381	632823	15.2	1813
1973	0.098	4458	783540	16.7	3221
1974	0.056	2682	192545	15.4	5282
1975	0.130	2854	780948	15.9	2423

the resulting fitted equation is:

$$\ln(N_0/E_M) = 2.567 \times 10^{-5} E_M + 1.5642 \times T_P - 1.769 \times 10^{-6} \times E_M \times T_P - 28.294 \qquad (29)$$

where variable E_M appeared to explain 73% of the variation, T_P explained 9%, and the interaction between temperature and eggs 5%. The equation can be rearranged to the form

$$N_0 = 5.151 \times 10^{-13} \times E_M \times \exp(2.567 \times 10^{-5} E_M - 1.769 \times 10^{-6} E_M \times T_P + 1.5642 T_P) \qquad (30)$$

Because of the auto-correlated nature of the fit the variation explained can be rather misleading. A better appreciation can be gained by observing Fig. 20. The partial correlations indicated that temperature explained nearly twice as much of the variation in year-class size as did egg numbers. As temperature increases, so does the height of the recruitment dome (Fig. 21), similar to the Ricker relationship (Ricker 1975, p. 284). Biologically this could be explainable by the effect of temperature on cannibalism. The higher the temperature, the quicker mackerel larvae reach metamorphosis and the sooner cannibalism stops and schooling behavior begins. Thus a large year-class survives. The growth mechanism in response to temperature, however, is also linked to the food supply. For egg production beyond the point at which the replacement line cuts all curves, higher temperatures result in smaller year-classes. This may be because the high cropping rate of mackerel on zooplankton leads to a diminished food supply and the young mackerel begin dying of starvation-induced predation; the higher the temperature, the higher the cropping rate and the smaller the year-class. Thus, at low egg productions, temperatures, and at high egg productions, temperature-controlled, density-dependent starvation after metamorphosis, may inhibit year-class success.

CONSTRUCTION OF THE SIMULATION

The simulation model was initially written in APL for 'debugging' and testing purposes and later rewritten in FORTRAN. The stochastic nature of the model and the many runs necessary to calculate the means and deviations for the different fishing strategies made the printing capabilities of APL extremely time-consuming and uneconomical. However, the explanation of how the simulation was constructed will relate to the APL model because of the ease of scientific-type programming in this language.

The actual model is a group of subprograms dealing with different aspects of the simulation procedure. A subprogram is a group of algorithms to facilitate linear interpolations (AFGEN), sampling from normal distributions (GAUSS), and a procedure whereby a probability is put in and a deviation is retrieved (INVGAUSS). The AFGEN algorithm is particularly useful since it allows the programmer to sample from any functional relationship. The subprogram COD0 is merely a description of variables utilized throughout the model while COD1 initialized the cod simulation.

COD1 begins by asking for the mackerel biomass in metric tons which is determined in program MAXK1, and for fishing mortalities in the winter and summer otter-trawl fisheries, gillnet fishery, and line fisheries. Furthermore, questions are asked concerning the length of time the simulation is to run, the number of runs, and type of output expected. Matrices are set up for the AFGEN program concerning the selection of the different gear types within the fishery. Later some calculations are made concerning ℓ_1 size, standing biomass and growth. In addition, the numbers-at-age x 10^3 are entered. The simulation is now passed onto the next subprogram COD2.

The program has been written so that the winter and summer fisheries can be conducted in a seasonal manner. This utilized the seasonal growth information and the seasonal distribution of the fishery.

COD2 is the main body of the simulation and contains the mathematical representation of the population energetic response of the southern Gulf of St. Lawrence cod stock. The model first enters a loop which represents the monthly update of the fishery between January and April (Fig. 22). The weight is calculated from the instantaneous growth by the equation

$$(i)\quad W_a = W_a \times \exp\ (G \times \text{GROWTH AFGEN GG})$$

so that the yearly growth rate is broken down into the appropriate monthly values (Fig. 23) by linear interpolation of cumulative GROWTH per month GG. GROWTH is a matrix of values representing the cumulative seasonal growth (Fig. 11). Once this value, expressed as a percentage, is determined it is multiplied by the instantaneous annual growth rate, G. The exponential of this value is multiplied by the current weight.

Next the length at age, L_a, is calculated from the weight at age, W_a,

$$(ii)\quad L_a = (1.0902 \times 10^5\ W_a)^{0.333}$$

then these lengths are used to calculate the selection at age for otter trawls,

$$(iii)\quad \partial a = \text{TRAWLMESH AFGEN } L_a$$

where TRAWLMESH is a matrix of values representing the selection pattern of otter trawls for different lengths-at-age. The fishing mortality value, FW_a, for the winter otter-trawl fishery is divided by four so the catch can be calculated on a monthly basis. This catch is calculated by the Baranov catch equation (Beverton and Holt 1957),

$$(iv)\quad {}_aCW_t = \sum_{a=3}^{a=15} \frac{N_a W_a\ (1 - \exp\ (-(FW + MW)) \times FW_a}{FW_a + MW}$$

where ${}_aCW_t$ is the winter otter-trawl catch and MW is the monthly natural mortality rate. The model is coded to accumulate the catch, updated by 1 mo, and looped to equation (i) until the simulated month of May.

The simulation now begins the recruitment phase. Since environmental factors affect the survival of cod eggs, spring temperatures (May 25 as a convention) are determined by sampling from a normal distribution with mean 4.84 and standard deviation 0.95. For this procedure, the algorithm GAUSS is used. In addition to temperature, the position of the maturity ogive in relation to length and age is important. It was shown earlier that the length at first maturity was related to the growth rate in the first year. The following equations describe shifts in the maturity ogive relation to ℓ_1 growth rate:

$$(v)\quad {}_tMLM = (99.09 \times \exp\ (-0.5571 \times \ln {}_t\ell_1) + 13.0$$

where MLM is the mean length at maturity and ℓ_1 is the length at the end of the first year. It was found that on average the mean length at maturity was 13 cm greater than the length at first maturity, therefore equation (iv) only supplies an approximation to the real situation. Since the mean length at maturity and standard deviation are known, actual maturities at age can be calculated by the relationship:

$$(vi)\quad {}_tMAT_a = \text{INVGAUSS}\ ({}_tL_a - {}_tMLM) \div 8$$

assuming a cumulative normal distribution.

The mature stock numbers are now calculated:

$$(vii)\quad {}_tMSN = \sum_{a=13}^{a=15} {}_tMAT_a \times {}_tN_a$$

and used to calculate the weighted average growth rate, ${}_tMGR$

$$(viii)\quad {}_tMGR = \sum_{a=3}^{a=15} {}_t\Delta W_a \times {}_tN_a \times {}_tMAT_a \div {}_tMSN$$

where the growth rate at age a in year t is:

$$(ix)\quad {}_t\Delta W_a = 6.6 \times {}_tBS^{-0.252} \times {}_tw_a^{-0.052} \times \ln {}_tBS_{s\,t}w_a$$

and ${}_tBS$ is the summer biomass after the winter fishery in year t.

The ${}_tMGR$ is now used to calculate the catch of cod eggs per 1 000 000 m^3 of water when coupled with previously mentioned spring water temperatures and ${}_tMSN$.

$$(x)\quad {}_tEGGS = 5.97 \times {}_tMGR^{1.22} \times \exp\ (1.678\ TP1^2) \times {}_tMSN \times 10^{-3}$$

This relationship suggests that there is an optimal temperature, TP, for egg survival and that temperature is indeed very important in determining final egg numbers.

It has previously been determined by Lett et al. (1975a) that increased temperature improves the survival of cod larvae. The following equation was developed to determine the number of cod larvae, LR, after a specific period of time:

$$(xi)\ \Delta LR = (1.639 \times 10^{-2} \ln LR \times (1-1.0683 \times 10^{-3} \times TP2^2) - 0.04854) \times LR \times \Delta t$$

where initially:

$$(xii)\ LR = {}_tEGGS$$

therefore:

$$(xiii)\ {}_{t+\Delta t}LR = {}_tLR + \Delta LR$$

for a particular time interval Δt.

The total time period in the simulation was 50 d and Δt equalled 1 d. TP2 is the maximum summer temperature in the Gulf, normally distributed with mean 14.39°C and standard deviation 1.28°C.

Predation by a mackerel biomass ${}_tMB$ and cannibalism by an average 3+ cod biomass when juvenile cod are 0-group and one ${}_{to,1}BC$ is shown to be important in conjunction with the abundance of cod larvae in the recruitment of cod. The year-class size of cod is predicted at age 3, N_3, since this is the first year of sampling data. The equation

$$(xiv)\ N = 4.220 \times 10^{-3} LR \times \exp[(1-1.409 \times 10^{-8} \times {}_{to,1}BC \times {}_tMB^{0.5}) + (-5.160 \times 10^{-3} \times LR) (1.457 \times 10^{-11} \times {}_{to,1}BC \times {}_tMB^{0.5} \times {}_tLR) + (2.584 \times 10^{-9} \times {}_tLR \times {}_{to,1}BC)]$$

where ${}_tLR$ was placed in the first position of the numbers-at-age vector and had to wait three simulated years before being utilized in equation (xiv).

Following the calculation of year-class size the ℓ_1 size of cod is determined by the following equation which included a spring temperature slightly higher than that used to determine the mortality of eggs:

$$(xv)\ {}_t\ell_1 = 111.69 {}_tN_3^{(0.022 \times \ln TP3 - 0.300)}$$

where TP3 = TP1 + 0.92.

After the recruitment and other biological factors are determined, the model calculates catches in the summer fishery. This fishery contains three gear types: lines (LL), gillnets (GN), and trawls (OT), which all compete with one another. Selections for each of these fisheries are calculated by using lengths to linearly interpolate in the AFGEN algorithm. The total fishing mortality is calculated as follows. Again this position of model is iterated on a monthly basis so the seasonality of the fishery can be taken into account (Fig. 10).

$$(xvi)\ ETOT_a = (\partial GN_a \times F_{WOT_a}) + (\partial GN_a \times FGN_a) + (\partial LL_a \times FLL_a)$$

where ∂ is the selection and F is the instantaneous fishing mortality for age a. Thus the total fraction of fish caught in this fishery is $(FTOT_a/FTOT_a+MS)$ where MS is the natural mortality in the summer fishery. MS is equal to 0.017 since this fishery is iterated monthly. Thus catch in each of the winter fisheries is given by the catch equation:

$$(xvii)\ {}_aCS_t(OT,GN,LL) = \sum_{a=3}^{a=15} N_aW_a \frac{[1-\exp(-(FTOF_a+MS))xF(OT,GN,LL)]}{FTOT_a + MS}$$

After the simulated month of December is completed the simulation progresses to the update section of the program.

Following the summer fishery the model goes through an update phase. The instantaneous growth rate is calculated by rearranging equation (ix) such that:

$$(xviii)\ {}_tt_a = 6.6 \times {}_tBS^{-0.252} \times {}_tw_a^{0.052 \times \ln {}_tBS}$$

Weight is updated by

$$(xix)\ {}_{t+1}W_{a+1} = {}_tW_a \times \exp {}_tG_a$$

A new weight is determined by the ℓ_1 length and placed on the front of the length vector and the age 16 fish are dropped from the vector. Next the numbers-at-age are updated by the expression

$$(xx)\ {}_{t+1}N_{a+1} = {}_tN_a \exp -(FTOT + MS)$$

and the number of larvae is put on the front of the abundance vector while age 16 fish are dropped.

At this point in the model a number of biological factors are accumulated to be subsequently printed out. The next subprogram COD is responsible for formulating the output into matrices and calculating means and standard deviations.

For the mackerel section of the program, MACKI, the programs were written so control is set at the beginning of COD1. Thus COD1 is the main program controlling input to both the mackerel and cod subsections. The input consists of the 1977 numbers-at-age in millions, the lengths-at-age in centimeters, the predicted length of the 1-group mackerel in centimeters, and the range of years over which the simulation is to be run.

The logic of the biological aspects of the model is depicted in the flow chart (Fig. 22). At the start of each year of the simulation the population numbers for that year, the lengths for the previous year, and the length of the 1-yr-olds for the current year are known.

The first step is then to calculate the change in weight (ΔW) between this year's weights and the previous year's weights. This is done by converting the previous year lengths (cm) to weights (kg) using the relationship:

$$(xxi)\ W_{t-1} = 2.908 \times 10^{-6} \times L_{t-1}^{3.384}$$

There is a relationship between the increase in weight divided by the previous year's weight and the previous year's weight as depicted in Fig. 23. A linear interpolation routine is used to obtain the value for $\Delta W/W_{t-1}$ and the current year's weights are calculated as:

$$(xxii)\quad W_t = W_{t-1} \times \left(1 + \frac{\Delta W}{W_{t-1}}\right)$$

The change in weights is then calculated as:

$$(xxiii)\quad \Delta W = W_t - W_{t-1}$$

The next step consists of calculating the number mature at age. The percentage maturity is dependent on length and so the weights-at-age for the current year are converted to length:

$$(xxiv)\quad L_t = 3.4 \times 10^{-5} (W_t)^{0.342}$$

The percentage maturity at age is distributed as a cumulative normal variate with mean 26.4 and standard deviation 1. The number mature at age is then simply the percentage mature times the numbers-at-age. No 1-yr-old fish are allowed to mature.

The next step consists of calculating the number of 0-group fish which will be produced and predicting their lengths when they reach age 1. The egg production is calculated as:

$$(xxv)\quad E_M = 6876 \times N \times (\Delta W)^{1.579}$$

with the summation being over all age groups. The number of 0-group mackerel depends on the number of eggs and the temperature. A random temperature (TP) is calculated based on the long-term observed temperature distribution. The number of 0-group fish is then calculated as:

$$(xxvi)\quad N_0 = 5.151 \times 10^{-13} \times E_M \exp(2.567 \times 10^{-5} EM - 1.769 \times 10^{-6} E_M \times T_P + 1.5642\ T_P)$$

There is a relationship between the number of 0-group fish and their length-at-age on L_1. The length at age 1 is predicted as:

$$(xxvii)\quad L_1 = 27.894 \times \exp(-2.531 \times 10^{-5} \times N_0)$$

The final step in each year then consists of calculating the catch using the standard Beverton-Holt catch equation

$$(xxviii)\quad C = \sum_{a=1}^{a=10} N \times \left(\frac{F}{F_a + 0.3}\right) \times [1 - \exp(-F_a - 0.3)]$$

where the summation is over all age groups.

The population numbers for the next year are then updated by taking the number of 0-group fish multiplied by exp(-0.3) and adding this to the front of the population vector for the older age groups which is calculated by multiplying the current population vector by exp(-F-0.3). This assumes that there is no fishing mortality on 0-group mackerel. The partial recruitment factors for older mackerel are entered from outside the simulation. The current year's lengths (equation ii) are then saved as the previous year's lengths, the year counter is updated, and if there are more years to be run the whole process is repeated.

RESULTS AND DISCUSSION

THE RECRUITMENT MECHANISM

The foregoing suggests that the recruitment mechanisms of cod and mackerel are closely associated with the growth characteristics of each species. Indeed, a mechanism has been identified whereby surplus energy can be channelled into gonadal growth (Fig. 14, 15) and egg production. Whether this pathway is utilized as a homeostatic mechanism in response to the density-dependent growth of the mature population seems to be a characteristic difference between the two species.

Density-dependent growth is perhaps tied into particle size of food eaten by certain species. Adult mackerel eat smaller particles than juveniles (MacKay 1976; Kulka and Stobo, unpubl.) whereas cod go through a number of growth stanzas, eating larger and larger particles (Powles 1958; Daan 1973). Therefore, it is difficult to describe an asymptotic length ($L\infty$) for cod until they reach a great age, but mackerel approach $L\infty$ very soon after the first year. Ware (1975a) has described a mechanism for pelagic fish that enables them to reach a size for optimal foraging in relation to the particle size of food eaten and it is suggested here that mackerel are a species characteristic of his arguments.

Mackerel are a highly mobile schooling fish, and if the plankton becomes depleted in one area they move to another. Mackerel feed over the Continental Shelf from Labrador to North Carolina and thus a plentiful supply of zooplankton should always be available to them. By specializing to feed on zooplankton, mackerel as a species have traded, in an adaptive sense, their ability to change length for the allocation of surplus energy to gonad production. Our data certainly support this idea, showing that gonadal size can vary dramatically on an annual basis; however, these changes cannot be related to population density.

If mackerel do not alter their egg production in response to population density then the determination of the limits of the population fluctuations must be during the early life history. Cod, on the other hand, are not locked into a particular food particle size. As they grow, larger and larger food items are available to them and they change their diet accordingly. It is not until bigger food items begin to become so scarce that it is inefficient to capture and eat them that growth begins to approach as asymptote (Kerr 1971). Indeed, Jones and Johnson (1976) have suggested that when no larger particles were available to eat it was a good time for gadoid fishes to mature.

Because larger food particles are less abundant and turn over much less quickly than zooplankton, overcropping can diminish the standing stock within a particular particle range. If it takes years for these prey animals to replenish themselves, a mechanism for density-dependent growth is easily hypothesized. Indeed, it is an observed fact (Fig. 9) that cod show density-dependent growth. However, annual changes in growth are much more easily detected in the younger, faster growing fish than in

older mature cod. In this regard, mackerel and cod are similar, since most surplus energy is being allocated to gonadal products; however, cod are still channelling a certain proportion into somatic growth.

Gonadal growth in cod is related to somatic growth (Waiwood, unpubl. data); therefore mechanisms leading to so-called density-dependent growth imply that a homeostatic function operates through egg production as well as somatic production. Cod, then, unlike mackerel, may have limits to their population fluctuation defined by the adult phase, based on carrying capacity of the benthic and semi-pelagic environment.

Both cod and mackerel show density-dependent growth in the first year, although the degree of dependence is much stronger for mackerel than for cod (equations 16 and 17). The reason for this difference is the rate at which the juvenile fish grow. On average, mackerel are growing 4-6 times faster than juvenile cod; thus the scale of response is much wider. The rate of growth affects the length at first maturity in cod (Fig. 13) but not in mackerel in which, considering the available data, length of first maturity seems to be fixed. However, the rate and flexibility of juvenile growth in mackerel allow the age at first maturity to be as plastic as that of cod. Thus, the population stability maintained through the eventual alteration in egg production is probably equal for both species.

If the early life history of mackerel is the factor which determines the ultimate size and variability of its population, then the key to annual variations in recruitment must also be determined in the first year. Thus the study of this phase will ultimately lead to the ability to predict year-class size. Herring, like mackerel, do not show density-dependent growth in the adult phase (Lett and Kohler 1976) but are cannibalistic, with the older stock eating larvae. The important cannibalistic mechanism for mackerel is the eating of small larvae by larger ones (Hunter and Sanchez, unpubl.). Cod tend to operate in a similar manner to herring, the older cod preying on juvenile cod as they become demersal. The important question, however, is which carrying capacity affects the amount of cannibalism. For cod, the environmental pressure on the adults ultimately must determine the year-class size, which has been shown not to be completely formed until the second year. For mackerel it is the interaction of food supply and cannibalism of larval and juvenile fish that ultimately forms the year-class, independently of the adult stock. The recruitment of herring seems to lie somewhere in between these two extremes with cannibalism of adults on larvae being important but not determinant through a mechanism involving their carrying capacity (Lett and Kohler 1976).

One aspect of recruitment is similar for mackerel, herring and cod in relation to their management. That is, year-class size is fairly independent of the production of larvae over a wide range of stock sizes. More of the variation is attributable to environmental factors, temperature in the case of mackerel, and predation by mackerel in the case of cod and herring, than to the biomass or growth rate of the adult stock. The more important factor is the effect of stock size in cod and herring and the predatory biomass of the stock to which the year-class will eventually recruit.

GENERAL PRODUCTION MODELS AND ENVIRONMENTAL VARIABILITY

Given any level of environmental randomness, population numbers and yield exhibit greater fluctuations as harvesting effort increases. This particular problem has been studied mathematically by Doubleday (1976), Sissenwine (1977), and Beddington and May (1977). Lett and Kohler (1976) and Lett and Benjaminsen (1977) have commented on the biological basis for such fluctuations in fisheries and their implication. The models presented for both mackerel and cod show similar results, and it is worthwhile restating the arguments. In addition, the interaction between cod and mackerel has substantial impact on the variance structure of the cod general production curve, with the results being rather contrary to conclusions expressed by other authors (Beddington and May 1977).

In the simulation, as the rate of fishing increases on mackerel so does the catch. The biomass declines (Fig. 24) until the maximum sustainable yield, MSY, is achieved. The simulated MSY for this stock is 450 000 MT, at a weighted fishing mortality of 0.4 and stock biomass of 1.4 million MT. After the MSY biomass is achieved, yield begins to fall off gradually skewing the relationship toward higher fishing mortalities. The direction of this skew is a result of the method in which negative feedback enters the model. Since the density-dependent 0-group growth relationship is a negative exponentive, the density-dependent effect in response to year-class size becomes less effectual at smaller stock sizes (egg production) (Fig. 11). At a stock size that approaches a critical stock size, density-dependent effect would go to zero very rapidly.

As the stock declines beyond what would be deemed as an MSY stock size, the variance in the catch begins to increase dramatically. This effect is primarily due to the relationship between egg production, year-class size, and the method in which environmental variability enters the model. As equation 30 and Fig. 21 suggest, the greatest effect of temperature occurs at stock sizes less than where the replacement line cuts the recruitment curves. Temperature, as a log normally distributed variable, enters the model through an exponential and gains in importance as the density-dependent effect of larvae on their food supply declines. As stated previously, there is an interaction between cannibalism and overcropping of other foods, the degree of which depends upon the initial number of larvae. At larval numbers where the overcropping of food is no longer a problem, temperature-controlled cannibalism has its greatest effect. At high temperatures the survival of mackerel larvae should increase exponentially in the same manner that growth responds to temperature, since the sooner larvae reach metamorphosis, the greater the survival of the year-class. Therefore, more variance enters the model at lower stock sizes, perturbing the exploitable biomass, and decreasing the predictability of catch.

The cod story can be portrayed in a similar manner (Fig. 25) although, in general, the variance in catch at different levels of biomass is far less than observed for mackerel. This is in part due to the fact that cod have four negative feedback mechanisms compared with two modelled for mackerel. Therefore, the mackerel population as a whole would be more susceptible to environmental perturbation than cod. The links between events in the early

life history and the adult stock are also less binding for mackerel than for cod, possibly because mackerel are migratory with almost unlimited resources while cod are bounded by a much more defined carrying capacity, forcing the population to equilibrate. Thus a stronger tendency toward equilibrium reduces the chances of overcropping the available resource.

For different stock levels of mackerel the MSY for cod changes (Fig. 25). However, the relationship is certainly not one-to-one. A threefold decline in the 2+ mackerel biomass only leads to an increase of 30% in MSY and 50% in virgin stock size of cod. Variance in catch increases at lower biomass levels since the number of density-dependent mechanisms operating is reduced as the fish reach their physiological limits in relation to growth and feeding. Variance builds up as the population can no longer damp out environmental effects entering through recruitment by altering the production of eggs, shifting maturity, cannibalizing juveniles, and varying 0-group growth. A 3+ biomass of 40 000 tons for cod could be considered a critical stock size, since at this level of biomass a constant rate of exploitation can lead to an ultimate recruitment failure.

The surprising conclusion is that mackerel can increase the variability in cod catch far more than all other environmental factors combined, at stock sizes of cod greater than the MSY stock size. At stock sizes less than MSY, different levels of mackerel biomass do not alter the catch as greatly. That is to say, when cod larvae are not as plentiful, mackerel predation has much less effect on year-class size formation. Possibly, this is due to the patchy nature of larval distribution. Decreasing the number of patches reduces the changes of a school of mackerel encountering them.

However, the major point here is that, if managing mackerel properly is impossible, our objective of a sustained cod fishery with little variation from year to year is not tenable. Furthermore, if variance in cod catch is far less at stock sizes below the MSY stock size (Fig. 25) then fishing at the optimal economic level of $F_{0.1}$ or 2/3 would be unrealistic, due to a substantial increase in variance.

In accordance with the objectives set out in the introduction, a model has been presented that deals with a number of different life history phases of both mackerel and cod. The basic mechanism of the recruitment process has been elucidated for both species, but much of the treatment has been more statistical than biological. By this I mean that in many cases the basic ecological mechanisms have not been described. However, now that they are identified, mathematicians and laboratory experimentalists can begin using the relationships set out in this paper to direct further studies, and perhaps find general solutions to the stock-recruitment mechanism.

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Table 1. Cohort analysis, numbers-at-age x 10^6, M = 0.3, for mackerel. Starting values in 1977 are based on a population estimate determined from the egg survey information.

Age	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
0	508	505	620	1426	3914	10070	3852	4451	2318	2484	1813	3221	5282	2423	3246	2629
1	812	377	375	460	1056	2900	7549	2853	3294	1714	1838	1341	2383	3911	1792	2402
2	646	592	279	270	335	766	2148	5415	2108	2285	1208	1344	858	1685	2582	1317
3	639	477	437	202	198	240	547	1543	3806	1518	1450	824	758	431	883	1607
4	-	465	353	321	148	143	163	359	1017	2400	1020	862	372	339	224	419
5	-	-	329	259	235	108	103	91	214	623	1317	690	443	190	166	92
6	-	-	-	232	189	171	78	65	63	137	294	652	350	232	91	78
7	-	-	-	-	159	134	123	52	46	41	73	145	318	165	115	44
8	-	-	-	-	-	102	95	91	37	30	23	34	82	144	79	50
9	-	-	-	-	-	-	51	70	65	20	20	14	16	39	64	30
10	-	-	-	-	-	-	-	33	50	40	11	8	7	7	18	28
11	-	-	-	-	-	-	-	-	18	34	23	5	3	3	3	2

Table 2. Fishing mortality (F) from cohort analysis M = 0.3 for mackerel.

Age	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
0	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.001	0.002	0.001	0.002	0.001	0.000	0.002	0.002	0.001
1	0.016	0.002	0.028	0.018	0.022	0.000	0.020	0.003	0.066	0.050	0.014	0.147	0.047	0.115	0.008	0.006
2	0.003	0.006	0.020	0.012	0.034	0.036	0.031	0.053	0.029	0.155	0.082	0.273	0.387	0.346	0.174	0.024
3	0.019	0.002	0.008	0.013	0.026	0.089	0.122	0.117	0.161	0.098	0.221	0.497	0.505	0.358	0.446	0.075
4	-	0.047	0.009	0.012	0.017	0.026	0.287	0.216	0.191	0.300	0.091	0.367	0.372	0.415	0.594	0.160
5	-	-	0.049	0.019	0.019	0.032	0.160	0.069	0.151	0.452	0.404	0.380	0.348	0.436	0.461	0.161
6	-	-	-	0.080	0.042	0.031	0.095	0.050	0.131	0.332	0.406	0.420	0.452	0.407	0.432	0.158
7	-	-	-	-	0.143	0.048	0.006	0.041	0.133	0.279	0.465	0.280	0.491	0.445	0.533	0.160
8	-	-	-	-	-	0.394	0.011	0.037	0.342	0.143	0.236	0.455	0.446	0.512	0.665	0.158
9	-	-	-	-	-	-	0.137	0.034	0.184	0.281	0.659	0.430	0.621	0.460	0.533	0.159
10	-	-	-	-	-	-	-	0.314	0.086	0.259	0.486	0.890	0.572	0.520	2.002	0.162
11	-	-	-	-	-	-	-	-	0.185	0.269	0.319	0.461	0.531	0.556	0.847	0.160

Table 3. Catch-at-age of cod, landed x 10^3.

Age	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
3	173	133	192	294	412	324	396	359	506	535	75	1	16	255	100
4	728	638	1034	2120	2968	2336	2372	2372	3341	3535	3967	3304	1720	2123	970
5	1559	1462	1915	5596	7832	6165	6727	6109	8607	9107	8983	13921	10887	4352	6728
6	2703	2113	3104	5037	7049	5549	6648	6037	8606	9000	12515	9475	1889	16021	5863
7	2772	2127	3065	4713	6596	5191	6331	5750	8101	8571	7144	8313	7870	14742	12038
8	2495	1874	2643	3799	5319	4186	5223	4743	6683	7071	1736	2661	4290	6390	9261
9	3327	2365	3141	3593	5029	3959	5381	4887	6885	7286	795	777	1480	3180	3760
10	2183	1582	2146	2680	3751	2952	3878	3522	4961	5250	1812	506	589	984	1133
11	901	638	843	942	1319	1038	1424	1293	1823	1929	388	741	153	392	347
12	478	351	483	636	890	701	902	819	1153	1221	279	385	178	137	149
13	138	106	153	235	329	259	316	287	405	428	76	188	37	102	103
14	128	94	130	173	243	191	245	222	314	332	93	174	26	37	88
15	79	58	80	106	148	117	150	136	192	203	51	33	36	50	24

Age	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
3	464	1498	700	310	327	26	2	1541	378	1229	2379	332	547
4	5504	7055	7068	8140	4936	3395	2476	14294	4396	3170	9902	4059	2733
5	6148	10689	5503	8086	12530	14972	7313	11326	11878	3862	6096	9089	3134
6	9292	4505	4586	4674	3571	11925	8941	7193	5982	9851	2350	4996	2266
7	4481	3423	3040	2916	2516	4194	6127	8479	4492	3631	3173	1513	1496
8	8524	1841	1735	1276	2136	1905	2567	5128	3455	2188	1250	834	400
9	5534	2262	407	753	917	1444	1237	1370	2204	2081	1033	423	269
10	1845	1890	1021	434	785	727	554	719	740	1186	738	220	193
11	1004	867	901	899	212	569	156	452	380	300	571	143	107
12	423	357	383	698	283	360	432	127	130	178	113	106	59
13	150	242	171	259	292	239	42	92	63	74	47	34	43
14	52	76	82	139	55	139	103	34	35	26	40	17	8
15	124	42	23	65	21	30	144	72	14	4	5	11	2

Table 4. Fishing effort (f) in trips, catch in metric tons (MT), and catch rates (CUE) for southern Gulf of St. Lawrence cod.

Year	Effort (trips)	Catch (MT)	CUE (MT/trips)
1950	3289	44023	13.38
51	2771	34827	12.57
52	3516	41956	11.93
53	6572	58911	8.96
54	6879	63901	9.29
1955	7592	65227	8.59
56	10004	104469	10.44
57	8917	89131	10.00
58	10804	86582	8.01
59	7706	70720	9.18
1960	12846	66013	5.14
61	9144	65583	7.17
62	8585	66664	7.77
63	9846	70202	7.13
64	9638	60547	6.28
1965	10786	63027	5.84
66	15039	54851	3.65
67	9562	41314	4.32
68	7146	46551	6.51
69	6438	47512	7.38
1970	8874	64459	7.26
71	11305	56375	4.99
72	13598	67733	4.98
73	13446	50635	3.77
74	19340	48736	2.52
1975	13741	39085	2.84
76	---------- data not available ----------		
77	4221	21096	4.99

Table 5. Selection-at-age for the weighted combination of the different gear types, for cod.

Age	1960	1961	1962	1963	1964	1965	1966	1967
3	0.619	0.000	0.022	0.236	0.330	0.748	0.572	0.301
4	0.753	0.678	0.385	0.343	0.562	0.696	0.664	0.722
5	0.891	0.722	0.593	0.615	0.696	0.750	0.846	0.857
6	0.956	0.859	0.764	0.801	0.776	0.810	0.899	0.871
7	0.989	0.964	0.909	0.894	0.894	0.906	0.962	0.938
8	0.989	1.000	0.992	0.969	0.972	0.943	0.982	0.952
9	0.956	0.992	1.000	1.000	1.000	0.995	1.000	0.931
10	0.975	0.872	0.807	0.939	0.929	1.000	0.988	0.977
11	0.754	0.776	0.386	0.810	0.740	0.934	0.908	1.000
12	0.299	0.457	0.817	0.603	0.775	0.769	0.766	0.993
13	0.247	0.271	0.527	0.887	0.337	0.535	0.544	0.817
14	0.113	0.167	0.287	0.611	0.551	0.789	0.441	0.885
15	0.598	0.324	0.092	0.934	0.287	0.734	0.394	0.531

Age	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
3	0.252	0.225	0.041	0.081	0.204	0.139	0.196	0.201	Not analyzed to date	0.118
4	0.616	0.563	0.590	0.651	0.437	0.470	0.615	0.606		0.467
5	0.876	0.842	0.752	0.818	0.744	0.774	0.851	0.849		0.831
6	0.968	0.942	0.909	0.891	0.912	0.901	0.973	0.972		0.814
7	0.969	0.954	0.940	0.912	0.939	0.961	1.000	0.997		0.724
8	0.953	0.988	0.918	0.932	1.000	0.995	0.994	0.995		0.831
9	0.957	0.969	0.941	0.960	0.964	1.000	0.930	0.938		0.747
10	1.000	1.000	0.931	0.941	0.913	0.976	0.998	1.000		0.943
11	0.999	0.952	0.958	0.931	0.779	0.920	0.880	0.889		0.905
12	0.983	0.871	0.925	0.893	0.778	0.802	0.811	0.820		0.953
13	0.941	0.685	0.841	1.000	0.779	0.507	0.651	0.663		0.963
14	0.931	0.955	0.765	0.604	0.838	0.945	0.055	0.055		0.995
15	0.471	0.741	1.000	0.823	0.919	0.671	0.198	0.197		1.000

Table 6. Cohort analysis, numbers-at-age x 10^3, M = 0.2, for cod.

Age	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
3	113987	109640	113532	108046	78707	70001	83924	106681	110471	143344	134847	46119	60134	41747	61261
4	76132	93168	89645	92779	88195	64067	57019	68353	87018	89988	116876	110335	37758	49219	33949
5	62446	61673	75703	72460	74043	69522	50340	44320	53817	68221	70478	92101	87345	29357	38376
6	41633	49716	49171	60247	54262	53534	51342	35128	30758	36274	47615	49574	63809	61662	20098
7	27950	31641	38792	37449	44769	38048	38809	36020	23298	17486	21555	27660	32015	49715	35988
8	17732	20376	23981	28987	26396	30685	26454	26046	24288	11745	6561	11184	15124	19090	27364
9	12106	12260	14987	17243	20295	16799	21336	16933	17033	13838	3218	3801	6749	8501	9848
10	6572	6901	7898	9428	10866	12066	10172	12599	9442	7116	4737	1915	2409	4186	4148
11	3552	3405	4219	4524	5294	5502	7208	4819	7129	3241	1567	2239	1110	1440	2537
12	1755	2093	2211	2691	2852	3141	3566	4613	2775	4187	908	932	1163	771	824
13	817	1004	1396	1373	1628	1530	1937	2103	3036	1229	2323	491	415	791	507
14	461	544	726	1005	912	1035	1018	1300	1463	2119	619	1833	232	306	555
15	346	261	360	477	666	527	675	612	864	913	1435	423	1344	167	217

Age	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
3	52155	61216	106187	94971	57488	53455	76274	30455	52562	60673	42499	76794	79630
4	50066	42281	48764	86305	77476	46771	43742	62446	23540	42692	48563	32642	62574
5	26917	36010	28233	33529	63295	58965	35221	33573	38193	15296	32085	30800	23053
6	25332	16475	19811	18136	20135	40484	34730	22220	17239	20522	9029	20753	16993
7	11150	12332	9413	12070	10619	13254	22356	20344	11684	8701	7889	5266	12471
8	18572	5074	7000	4956	7244	6418	7057	12759	8984	5501	3839	3588	2942
9	14024	7493	2489	4161	2903	3998	3531	3455	5807	4230	2524	2012	2183
10	4661	6475	4088	1669	2726	1547	1967	1772	1589	2760	1580	1132	1265
11	2371	2147	3591	2423	974	1521	609	1109	800	631	1187	626	728
12	1763	1033	973	2125	1171	606	731	357	499	311	246	455	383
13	540	1061	523	450	1108	702	170	208	178	291	94	99	277
14	322	306	650	273	134	643	359	102	87	89	172	34	50
15	375	217	182	458	98	60	401	201	53	39	49	104	13

Table 7. Fishing mortality (F) from cohort analysis, M = 0.2, for cod.

Age	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963	1964
3	0.002	0.001	0.002	0.003	0.006	0.005	0.005	0.004	0.005	0.004	0.001	0.000	0.000	0.007	0.002
4	0.011	0.088	0.013	0.026	0.038	0.041	0.052	0.039	0.043	0.044	0.038	0.034	0.052	0.049	0.032
5	0.028	0.027	0.028	0.089	0.124	0.103	0.160	0.165	0.194	0.160	0.152	0.183	0.148	0.179	0.215
6	0.074	0.048	0.072	0.097	0.155	0.122	0.154	0.211	0.365	0.320	0.343	0.237	0.034	0.338	0.389
7	0.116	0.077	0.091	0.150	0.178	0.163	0.199	0.194	0.485	0.780	0.456	0.404	0.317	0.397	0.462
8	0.169	0.107	0.130	0.156	0.252	0.163	0.246	0.225	0.363	1.095	0.346	0.305	0.376	0.462	0.468
9	0.362	0.240	0.263	0.262	0.320	0.302	0.327	0.384	0.592	0.872	0.319	0.256	0.278	0.518	0.585
10	0.458	0.292	0.357	0.377	0.481	0.315	0.541	0.370	0.869	1.394	0.550	0.345	0.315	0.301	0.359
11	0.329	0.232	0.250	0.262	0.322	0.234	0.246	0.352	0.332	1.072	0.320	0.455	0.165	0.358	0.164
12	0.358	0.205	0.276	0.303	0.423	0.283	0.328	0.218	0.615	0.389	0.415	0.610	0.185	0.219	0.223
13	0.207	0.124	0.129	0.210	0.253	0.207	0.199	0.163	0.160	0.486	0.037	0.550	0.104	0.154	0.254
14	0.367	0.212	0.221	0.211	0.349	0.228	0.309	0.209	0.271	0.190	0.182	0.111	0.132	0.144	0.193
15	0.289	0.280	0.280	0.280	0.280	0.280	0.280	0.280	0.280	0.280	0.040	0.090	0.030	0.400	0.130

Age	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
3	0.010	0.027	0.007	0.004	0.006	0.001	0.000	0.058	0.008	0.023	0.064	0.005	0.008
4	0.130	0.204	0.175	0.110	0.073	0.084	0.065	0.292	0.231	0.086	0.255	0.148	0.049
5	0.291	0.398	0.243	0.310	0.247	0.329	0.261	0.467	0.421	0.327	0.236	0.395	0.162
6	0.520	0.360	0.296	0.335	0.218	0.394	0.335	0.443	0.484	0.756	0.339	0.309	0.159
7	0.587	0.366	0.442	0.311	0.304	0.430	0.361	0.617	0.553	0.618	0.588	0.382	0.141
8	0.708	0.513	0.320	0.335	0.394	0.398	0.514	0.587	0.553	0.579	0.446	0.297	0.162
9	0.573	0.406	0.199	0.223	0.430	0.509	0.490	0.577	0.544	0.785	0.602	0.265	0.146
10	0.575	0.390	0.232	0.339	0.383	0.733	0.373	0.595	0.723	0.644	0.726	0.242	0.184
11	0.631	0.591	0.325	0.528	0.275	0.534	0.333	0.599	0.745	0.745	0.759	0.291	0.177
12	0.308	0.482	0.571	0.451	0.311	1.071	1.061	0.500	0.340	1.002	0.712	0.298	0.186
13	0.367	0.291	0.449	1.012	0.344	0.472	0.319	0.676	0.499	0.330	0.812	0.481	0.188
14	0.197	0.321	0.150	0.829	0.605	0.273	0.382	0.465	0.595	0.394	0.299	0.806	0.194
15	0.450	0.240	0.150	0.170	0.270	0.790	0.500	0.500	0.350	0.120	0.120	0.124	0.195

Table 8. Catch rate of 2+ cod caught in groundfish surveys in the southern Gulf of St. Lawrence and 3+ numbers-at-age from cohort analysis.

Year	CUE 2+ cod Gulf survey year t	CUE 2+ cod 3-yr average	Numbers of 3+ from cohort analysis year t+1
1962	189	170	266 945 x 10^3
63	133	156	235 666
64	145	125	208 242
1965	95	112	192 111
66	95	161	231 893
67	291	181	261 517
68	155	181	245 352
69	95	132	228 406
1970	144	96	227 120
71	48	92	189 026
72	84	62	161 273
73	52	58	161 729
74	37	61	149 755
1975	94	87	174 837
76	128	149	202 569
77	223	191	-

Table 9. Catch rate of 2-yr-old cod from groundfish surveys and the abundance of 3-yr-old cod of the same year-class, as estimated by cohort analysis.

Year-class	CUE age 2	VPA estimated at age 3 x 10^3
1957	17.32	134 847
58	3.10	46 119
59	3.53	60 134
1960	3.68	41 739
61	4.86	61 261
62	3.63	52 501
63	4.58	61 429
64	16.87	107 042
1965	6.92	95 111
66	7.53	56 944
67	2.04	50 480
68	6.96	74 245
69	0.62	23 460
1970	3.63	45 780
71	6.98	69 137
72	2.54	42 135
73	8.90	80 814
74	9.41	83 915
1975	26.42	187 363

Table 10. Weights-at-age (kg) of cod in 4T(Vn) for January.

Age	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	1962	1963
2	0.06	0.07	0.06	0.06	0.07	0.07	0.06	0.05	0.06	0.06	0.05	0.06	0.06	0.06
3	0.22	0.22	0.22	0.22	0.22	0.24	0.24	0.21	0.21	0.20	0.21	0.18	0.18	0.21
4	1.02	0.97	0.87	0.91	0.79	1.11	0.93	0.98	0.90	0.83	0.70	0.77	0.69	0.63
5	1.04	1.14	1.14	1.12	1.00	1.17	1.43	1.22	1.17	1.04	1.00	0.84	1.15	0.61
6	1.33	1.14	1.48	1.42	1.31	1.57	1.63	1.78	1.51	1.31	1.43	1.23	1.02	0.90
7	1.45	1.70	1.82	1.94	1.59	2.08	1.96	1.96	1.86	1.62	1.75	1.54	1.37	1.15
8	1.62	1.91	1.91	2.20	1.96	2.74	2.79	2.54	2.17	2.03	2.13	2.22	1.89	1.71
9	1.97	2.13	2.00	2.39	1.95	3.34	3.45	3.31	2.59	2.42	2.90	2.98	3.01	2.67
10	2.17	2.60	2.44	2.70	2.23	3.55	3.75	4.09	3.20	2.80	2.66	2.95	3.04	3.38
11	2.55	2.80	2.38	2.36	2.29	3.15	4.20	4.48	3.40	3.27	3.56	3.51	5.80	6.72
12	4.20	3.81	3.13	2.89	2.90	4.09	4.09	4.15	4.73	4.29	3.85	3.24	4.65	6.58
13	4.36	3.49	3.41	3.73	2.95	5.07	4.84	5.22	4.56	8.06	4.76	10.70	8.96	5.37
14	2.69	4.05	4.06	4.52	2.15	4.53	-	3.89	4.58	7.73	4.49	9.29	11.76	8.91
15	3.57	4.55	3.85	4.20	2.09	6.23	4.95	4.79	7.10	6.42	7.03	9.73	10.47	10.25

Age	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973	1974	1975	1976	1977
2	0.05	0.05	0.05	0.05	0.06	0.07	0.07	0.06	0.09	0.07	0.04	-	-	0.06
3	0.20	0.22	0.22	0.19	0.21	0.26	0.23	0.23	0.25	0.30	0.27	0.38	0.27	0.23
4	0.65	0.77	0.73	0.63	0.67	0.55	0.47	0.43	0.52	0.53	0.57	0.56	0.57	0.48
5	0.69	0.77	0.92	0.85	0.90	0.86	0.80	1.01	0.81	0.85	0.88	0.93	0.95	1.03
6	0.74	0.82	1.07	1.30	1.29	1.22	1.33	1.25	1.23	1.12	1.37	1.42	1.39	1.66
7	0.96	1.06	1.46	1.69	1.82	1.64	1.91	1.84	1.43	1.43	1.86	1.96	1.80	2.41
8	1.21	1.13	1.56	1.71	2.82	2.21	2.94	2.36	2.15	1.77	2.31	2.33	2.35	3.50
9	1.42	1.58	1.88	2.68	2.32	1.90	2.64	2.19	3.43	2.41	2.46	2.65	2.65	4.28
10	3.95	2.38	1.94	2.38	2.74	1.92	4.79	4.61	3.99	2.95	3.07	2.82	3.35	4.87
11	4.25	3.62	2.52	2.39	2.33	2.07	2.85	4.61	3.81	3.46	5.13	2.67	4.25	6.24
12	5.10	4.97	5.29	4.54	4.26	3.11	3.32	3.80	7.08	4.19	5.79	4.23	3.63	5.68
13	11.33	11.40	7.82	5.29	6.37	6.23	6.46	5.93	6.19	5.81	8.23	9.26	4.44	5.97
14	8.44	13.33	11.35	5.94	7.02	4.65	6.29	8.30	5.54	6.25	4.91	6.44	7.16	6.00
15	13.83	10.47	9.73	8.38	10.73	5.86	6.29	6.89	4.13	6.85	8.09	6.55	10.56	6.00

Table 11. Mackerel length-at-age (mm) in Div. 4X during July, August, and September of the year indicated.

Age	1965	1966	1967	1968	1969	1970	1971	1972[a]	1973[b]	1974	1975	1976	1977
1	265	281	264	221	253	250	260	(no value)	(no value)	242	239	265	233
2	320	309	296	287	272	299	291	310	293	259	280	310	302
3	341	336	333	328	314	316	305	320	321	321	320	320	324
4	350	341	345	342	337	330	319	335	336	339	343	343	336
5	355	356	355	352	355	345	333	334	345	350	363	355	351
6	352	360	357	356	354	358	348	336	348	358	369	369	360
7	-	355	364	361	368	358	368	360	362	361	373	374	378
8	-	356	369	369	383	381	366	380	369	370	388	379	378
9	-	-	-	384	380	387	385	376	392	385	396	382	384
10	-	-	-	390	385	382	400	400	388	393	388	385	387
11	-	-	-	-	-	-	-	-	-	403	409	394	385

[a]Lengths interpolated from Walford Plot.
[b]Age of these mackerel is uncertain since it seemed aging was incorrect by 1 yr.

Table 12. Weight-at-age (g) for mackerel samples in Subarea 4 fishery during July, August and September.

Age	1965	1966	1967	1968	1969	1970	1971	1972[a]	1973[b]	1974	1975	1976	1977
1	181.9	218.8	179.7	102.6	152.2	151.3	171.2	(no value)	(no value)	129.9	137.7	186.0	131.5
2	329.7	295.2	257.8	233.9	193.7	266.1	244.9	296.0	265.4	168.3	234.1	287.5	311.3
3	402.9	384.5	373.8	356.4	312.1	316.9	293.4	325.0	359.7	346.7	365.7	354.3	390.7
4	437.4	402.9	418.0	406.6	394.8	363.3	328.1	371.9	418.5	416.8	463.6	449.2	440.3
5	457.4	461.5	457.4	445.3	469.3	418.0	376.1	368.7	461.1	463.8	558.3	505.2	510.3
6	445.3	478.0	465.6	461.5	464.9	469.7	432.7	375.2	474.0	503.1	593.2	576.7	551.8
7	-	457.4	495.0	482.2	528.9	469.7	516.8	459.7	540.8	519.0	613.4	603.8	650.3
8	-	461.5	516.7	516.7	604.0	571.6	508.0	539.1	575.4	564.1	702.0	631.8	651.9
9	-	-	-	585.9	588.5	600.5	596.7	522.5	705.4	653.8	752.1	649.1	683.6
10	-	-	-	615.3	614.6	576.3	673.8	627.0	679.8	697.5	704.9	666.7	700.6
11	-	-	-	-	-	-	-	-	-	759.6	843.1	721.5	688.3

[a]Lengths interpolated from Walford Plot.
[b]Age of these mackerel is uncertain since it seemed aging was incorrect by 1 yr.

Table 13. Observed numbers-at-age of cod estimated from cohort analysis, and estimated values calculated using equation 27.

Year	Observed $N_3 \times 10^3$	Estimated $N_3 \times 10^3$
1954	106 681	129 949
1955	110 471	106 851
56	143 344	133 810
57	134 847	120 288
58	46 119	49 883
59	60 119	59 118
1960	41 739	51 151
61	61 261	51 589
62	56 163	60 634
63	61 261	63 933
64	107 042	75 327
1965	95 111	78 275
66	56 944	83 675
67	50 480	64 991
68	74 245	52 787
69	23 460	30 443
1970	45 780	57 786
71	69 137	41 877
72	42 135	44 931

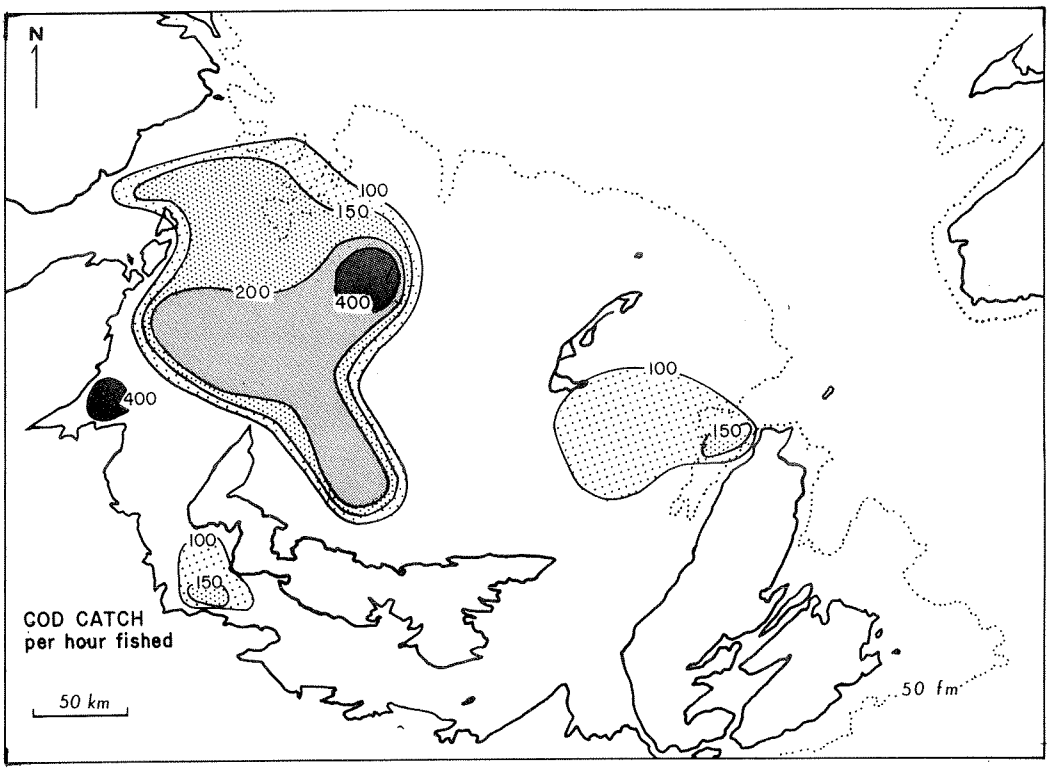

Fig. 1. Autumn distribution of cod in the Gulf of St. Lawrence determined by fall research surveys between 1970 and 1976. Values are the average kilogram per ton.

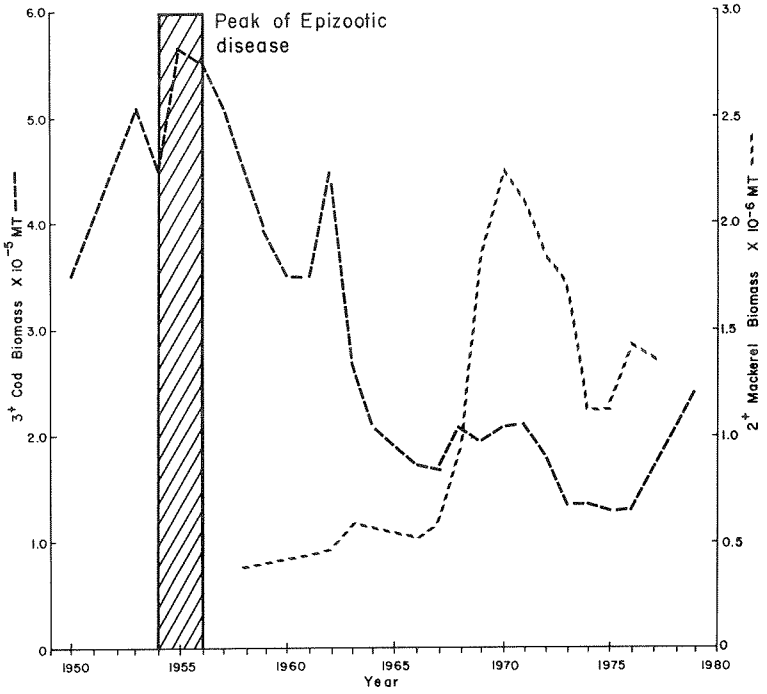

Fig. 2. 3+ cod and 2+ mackerel biomass over time as determined by cohort analysis in this study.

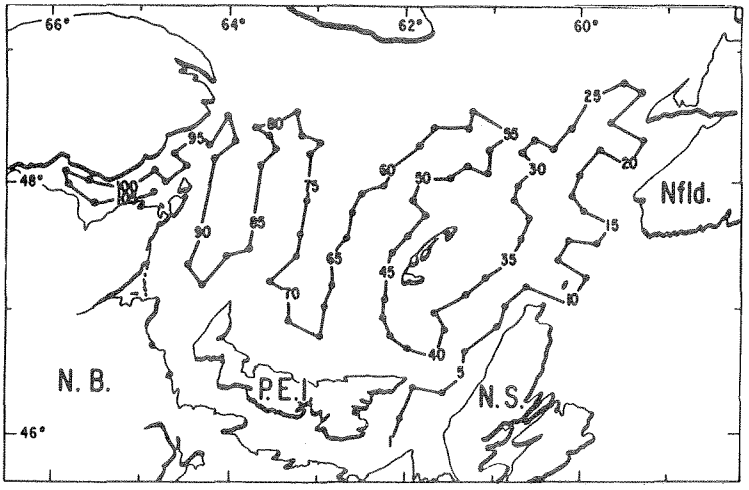

Fig. 3. Typical cruise track of Gulf of St. Lawrence egg and larval surveys adopted after 1967.

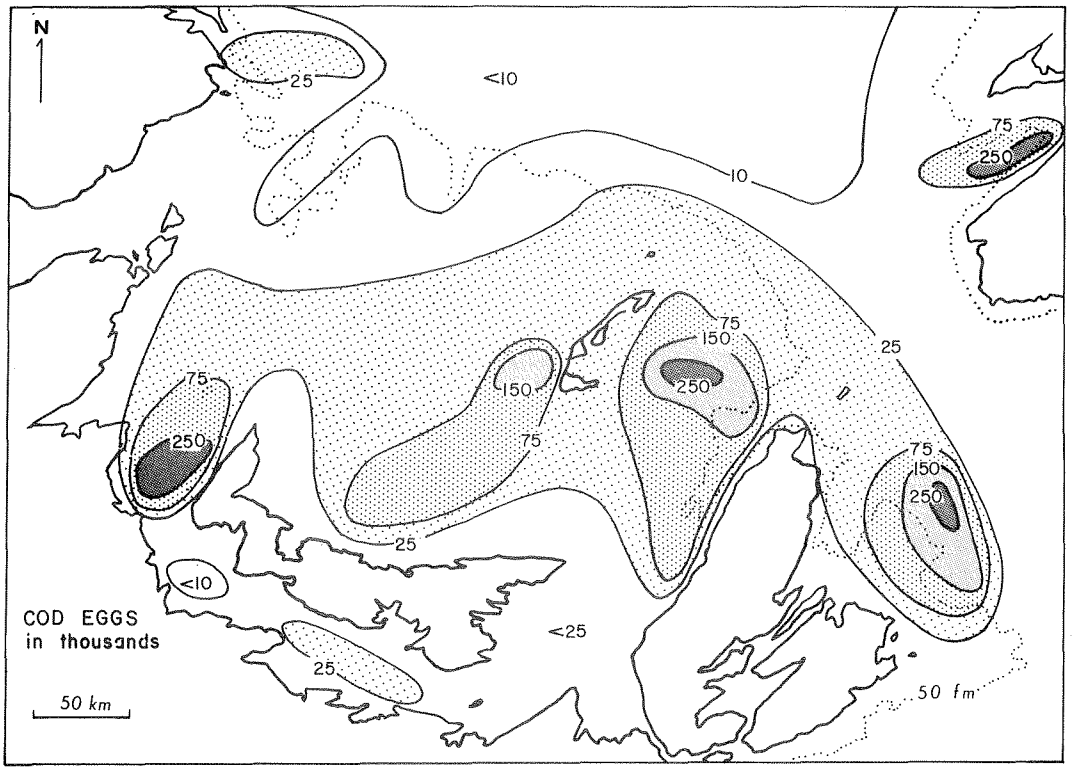

Fig. 4. Average distribution of cod eggs in the Gulf of St. Lawrence during the peak spawning period. Units are thousands of eggs per 10^5 m^{-3} water.

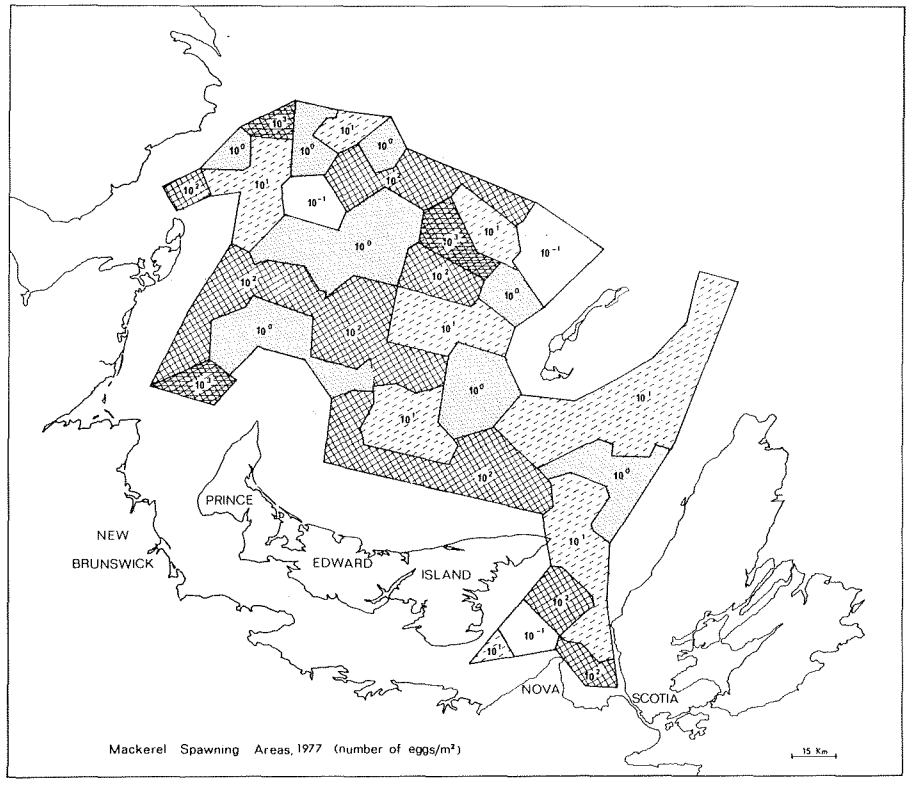

Fig. 5. Distribution of mackerel eggs per square meter of surface water in the Gulf of St. Lawrence.

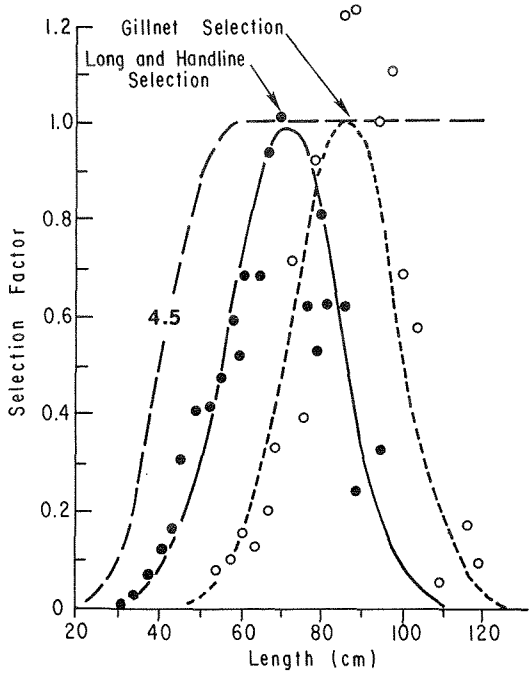

Fig. 6. Selection of different gear types in the southern Gulf of St. Lawrence cod fishery. Curve marked 4.5 refers to trawl selection.

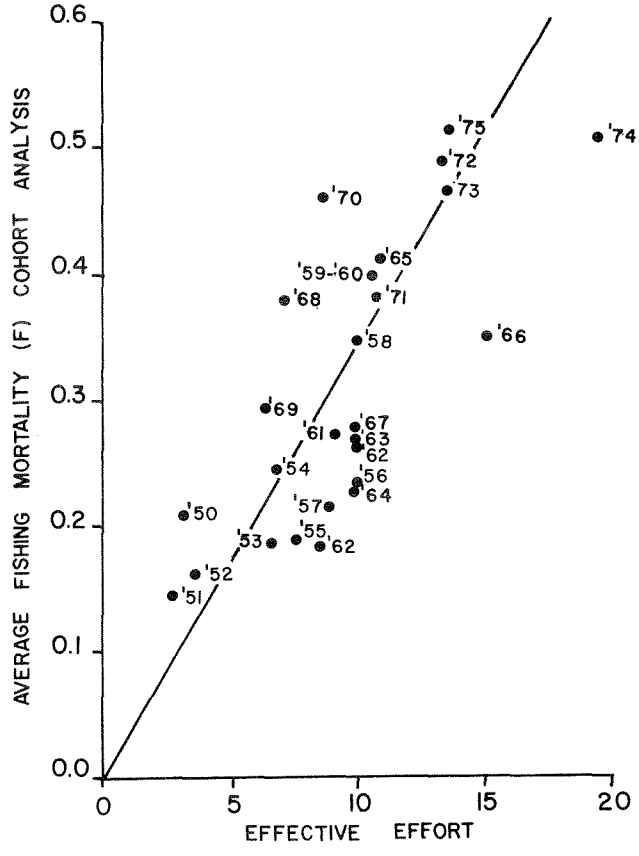

Fig. 7. Average fishing mortality from cohort analysis age 3-15 cod versus effective effort x 10^3.

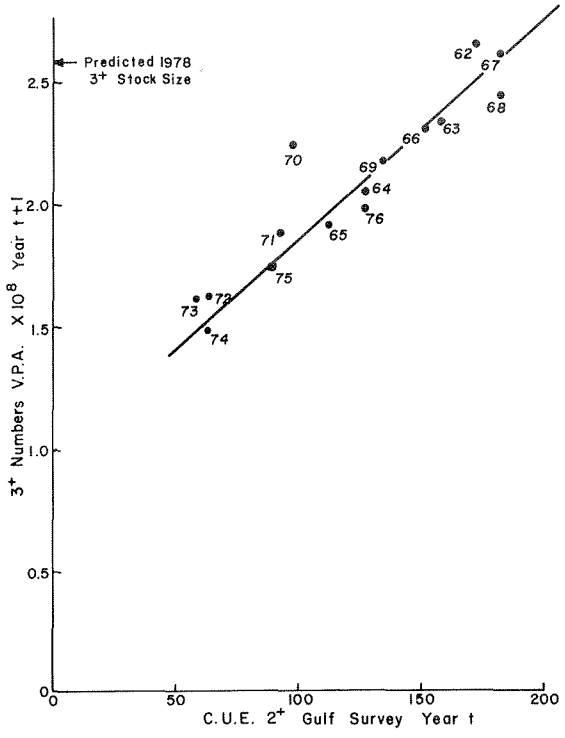

Fig. 8. Relationship between the estimated number of 3+ cod from cohort analysis and CUE 2+ cod caught in the fall of the previous year in the Gulf surveys.

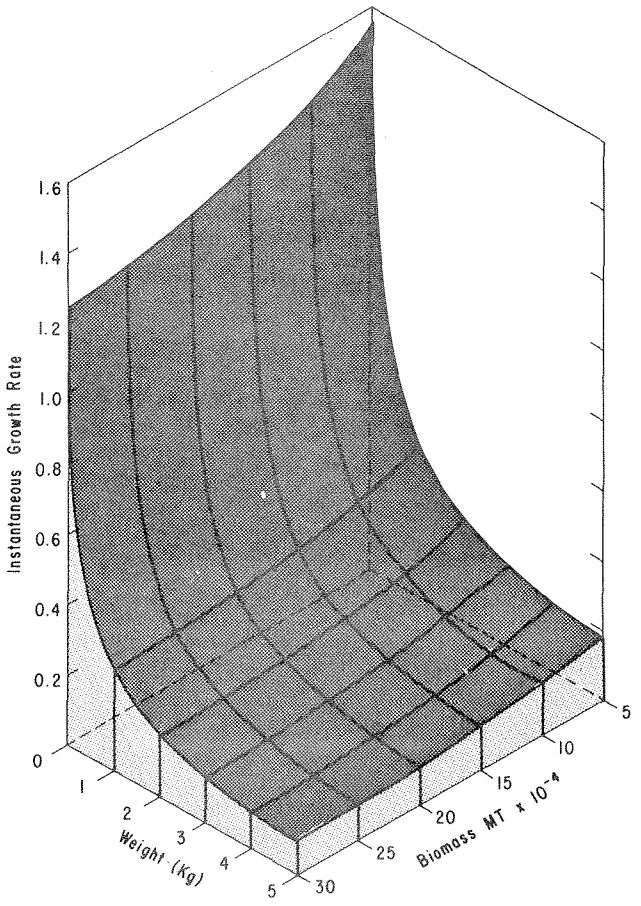

Fig. 9. Relationship among instantaneous growth rate, biomass and weight showing density-dependent growth in the Gulf of St. Lawrence cod.

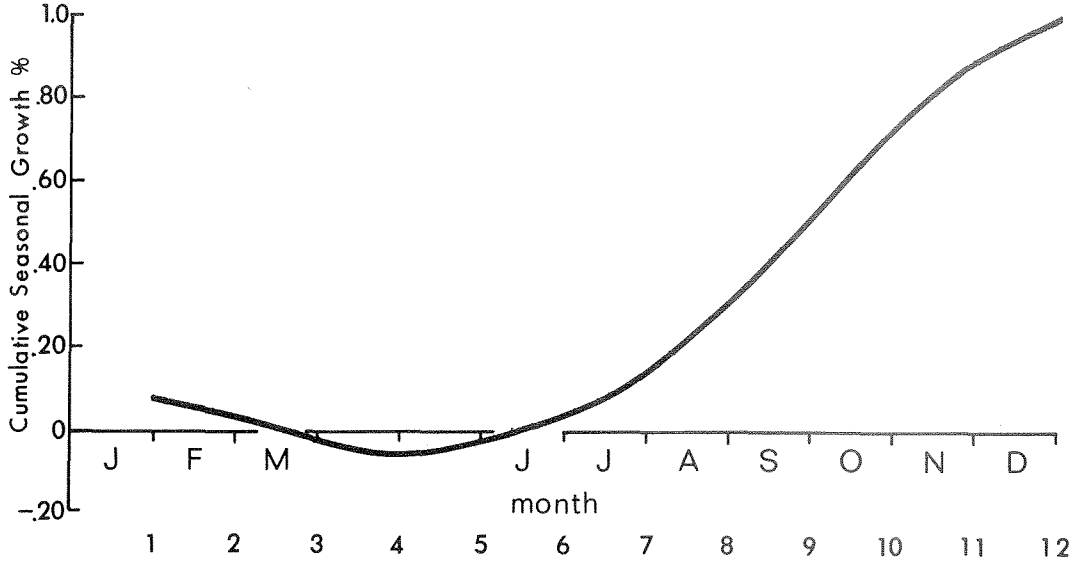

Fig. 10. A cumulative seasonal growth pattern for cod based upon laboratory experimentation by Waiwood (unpubl data); see text for explanation of relationship.

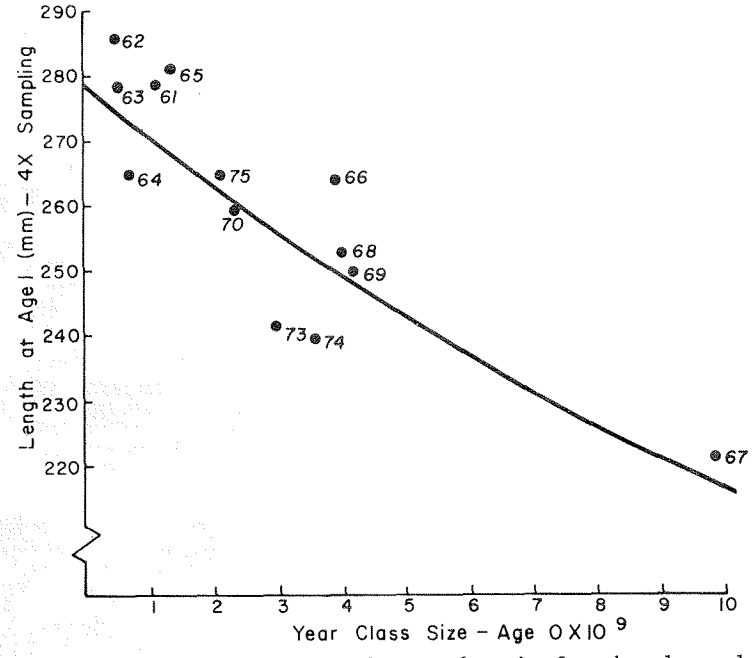

Fig. 11. Relationship between 0-group length of mackerel sampled in Div. 4X and year-class size.

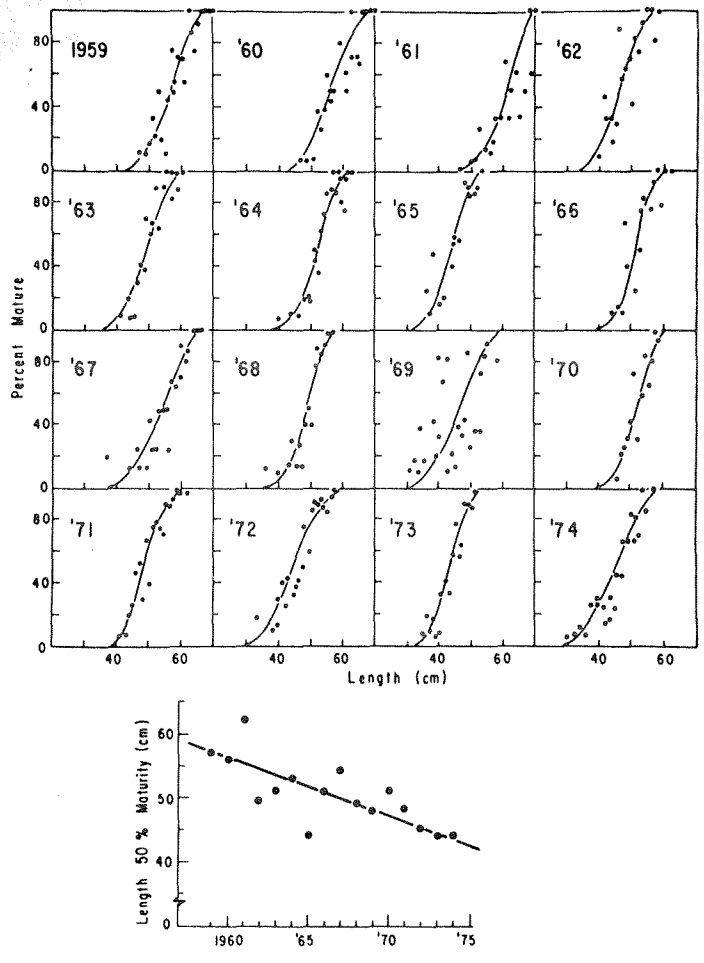

Fig. 12. Maturity ogives for female cod in the Gulf of St. Lawrence between 1959 and 1974.

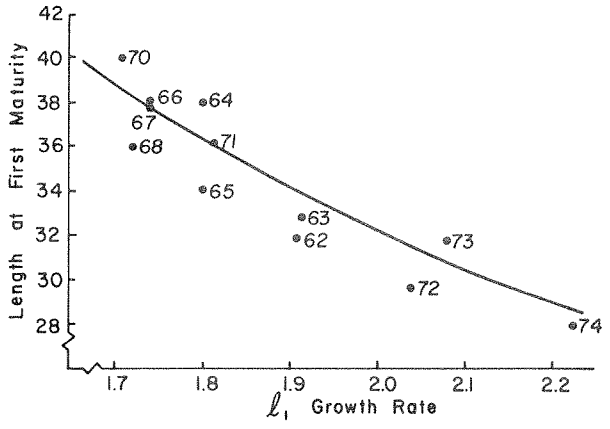

Fig. 13. The mean length at maturity of Gulf of St. Lawrence cod as a function of the ℓ_1 growth rate (cm).

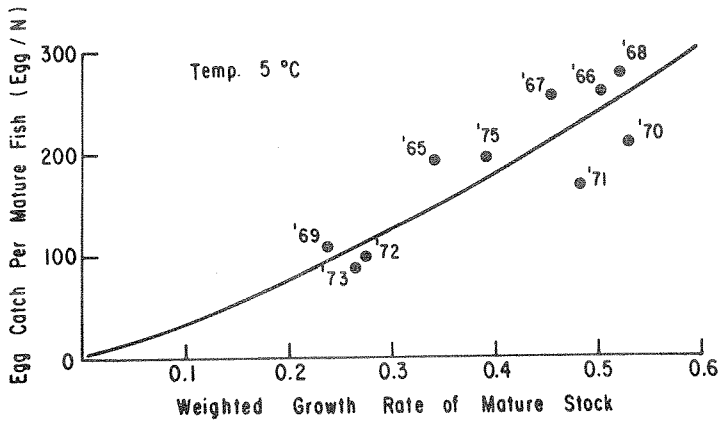

Fig. 14. The relationship among weighted mean, growth rate of mature cod, and egg catch per mature individual in the southern Gulf of St. Lawrence. The line is computed from equation 20 by using 5°C.

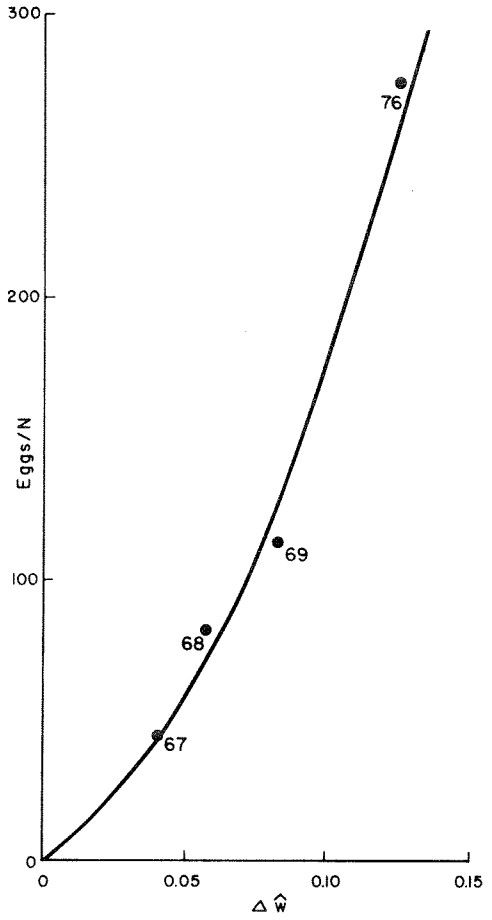

Fig. 15. Relation between the weighted mean growth rate, $\Delta\hat{W}$, (in g/yr) and the catch of eggs per mature mackerel.

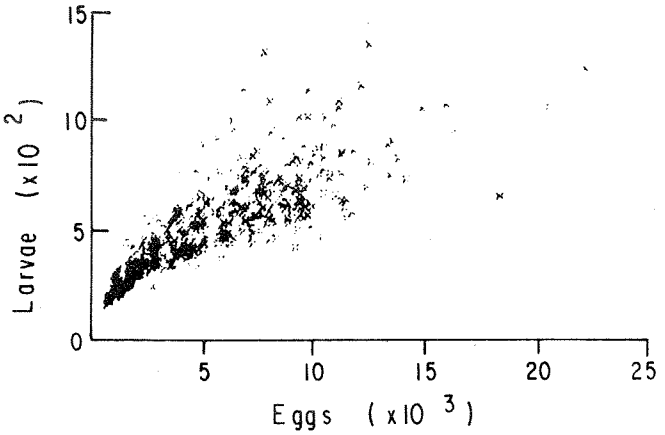

Fig. 16. Simulated relationship between the number of cod eggs at peak spawning and the numbers of larvae 50 d later. Temperature is varied as in equation 26.

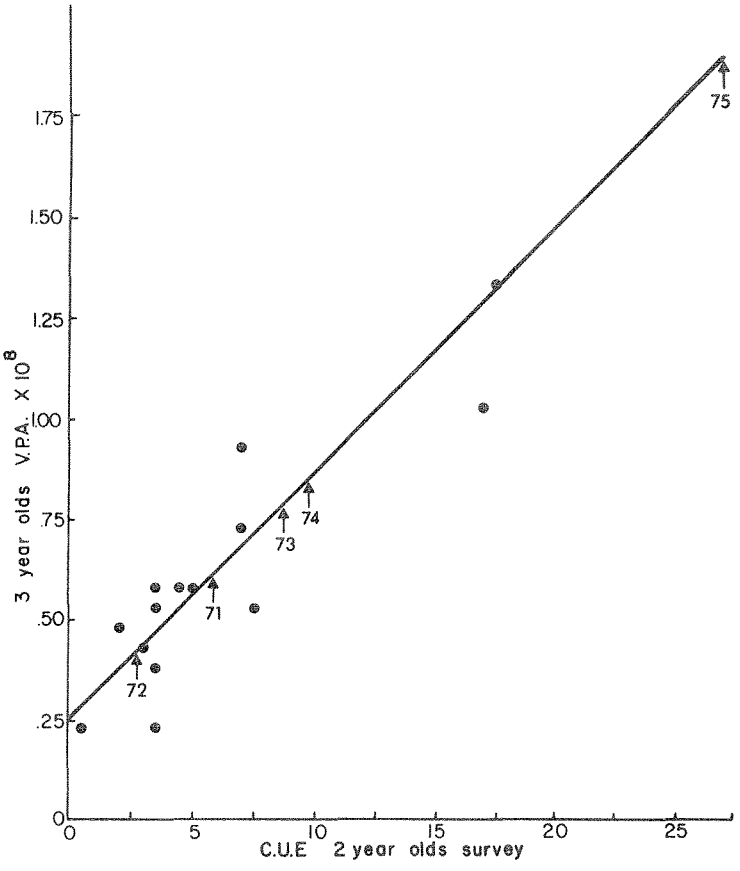

Fig. 17. Relationship between the catch of 2-yr-old cod in the Gulf surveys and the year-class size-at-age from cohort analysis. Arrows are predicted values based upon the CUE of 2-yr-olds in the Gulf survey.

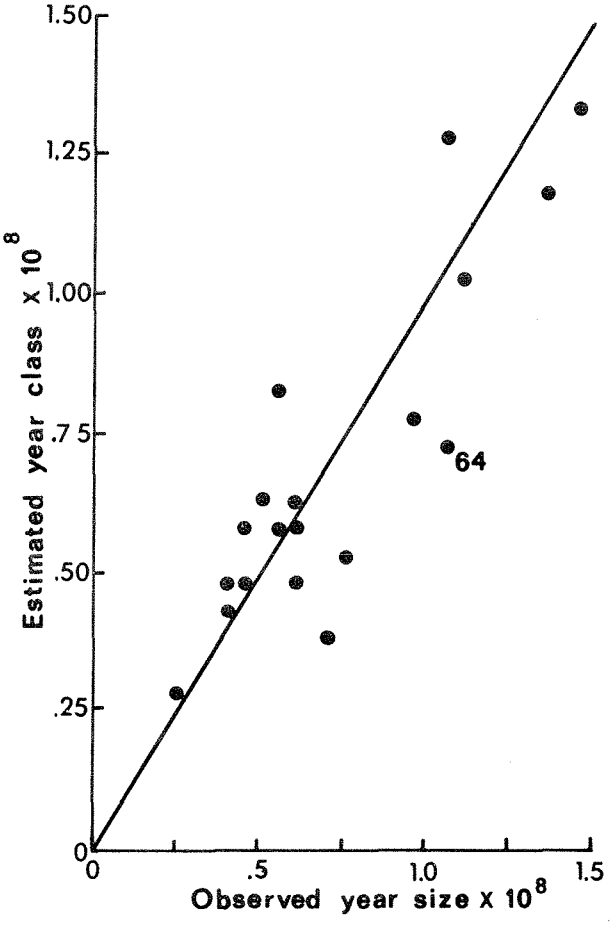

Fig. 18. The relationship between observed and estimated year-class size of cod, using equation 28.

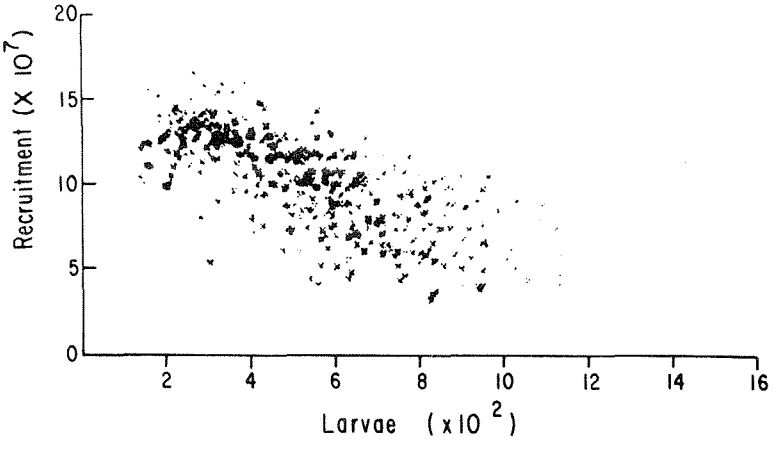

Fig. 19. Relationship between year-class size of cod x 10^7 and larvae for a fixed mackerel biomass and variable cod biomass.

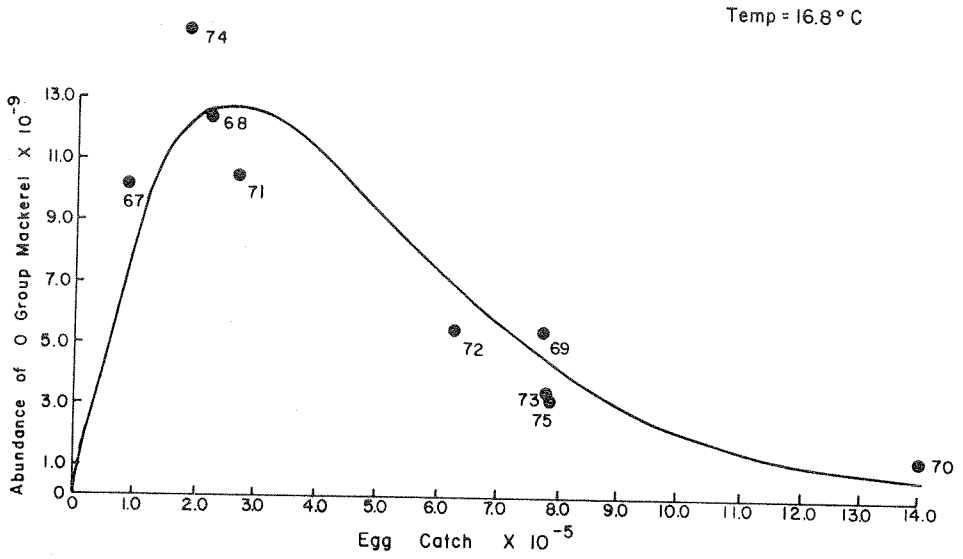

Fig. 20. Relationship between year-class size in mackerel (0-group) and egg catch from the adult stock. Relationship has been adjusted to a temperature of 16.8°C.

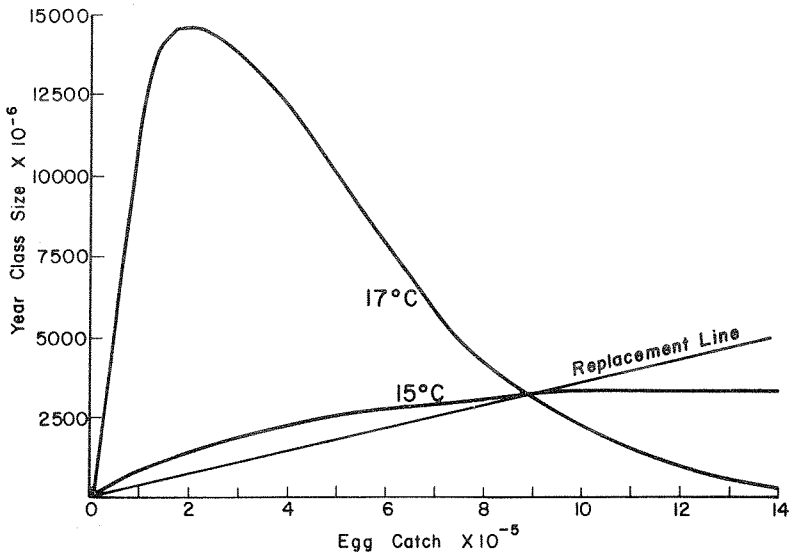

Fig. 21. Two stock-recruitment curves for mackerel showing effects of variable temperature based on the relationship described by equation 31.

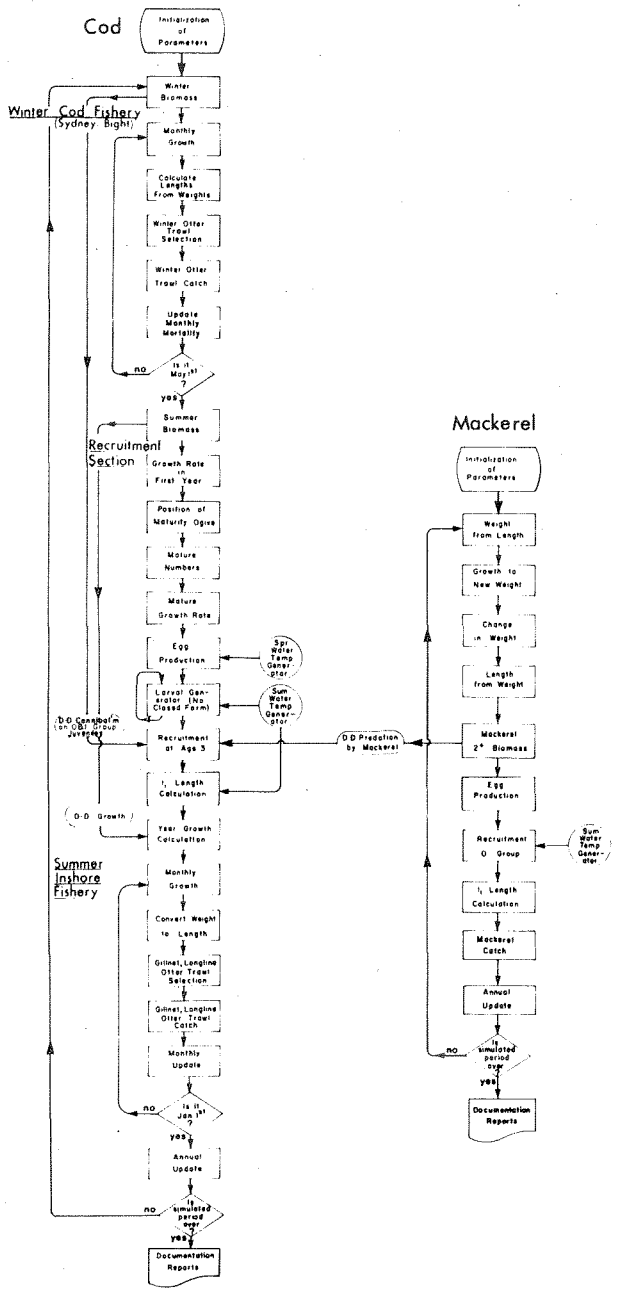

Fig. 22. Flow chart of system simulation of cod and mackerel fishery.

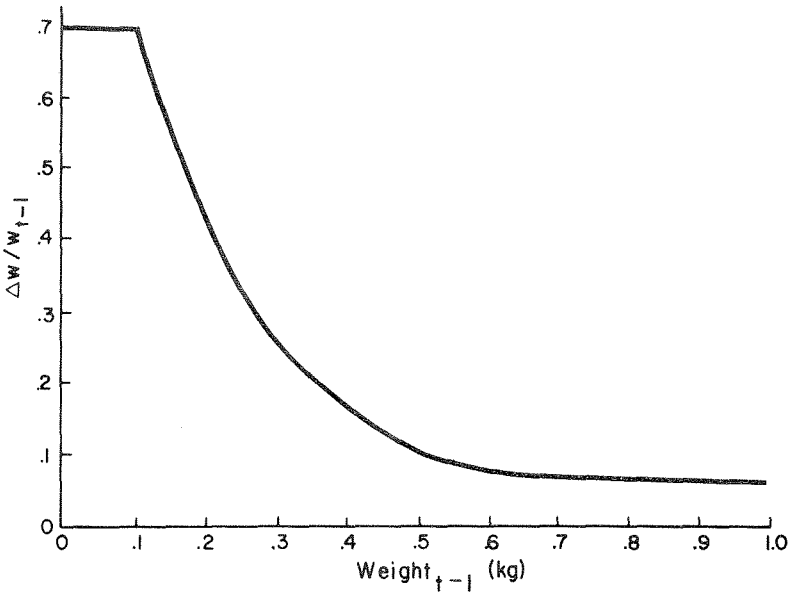

Fig. 23. Simulated relationship between change in weight in the current year (ΔW) divided by weight in the previous year (W_{t-1}).

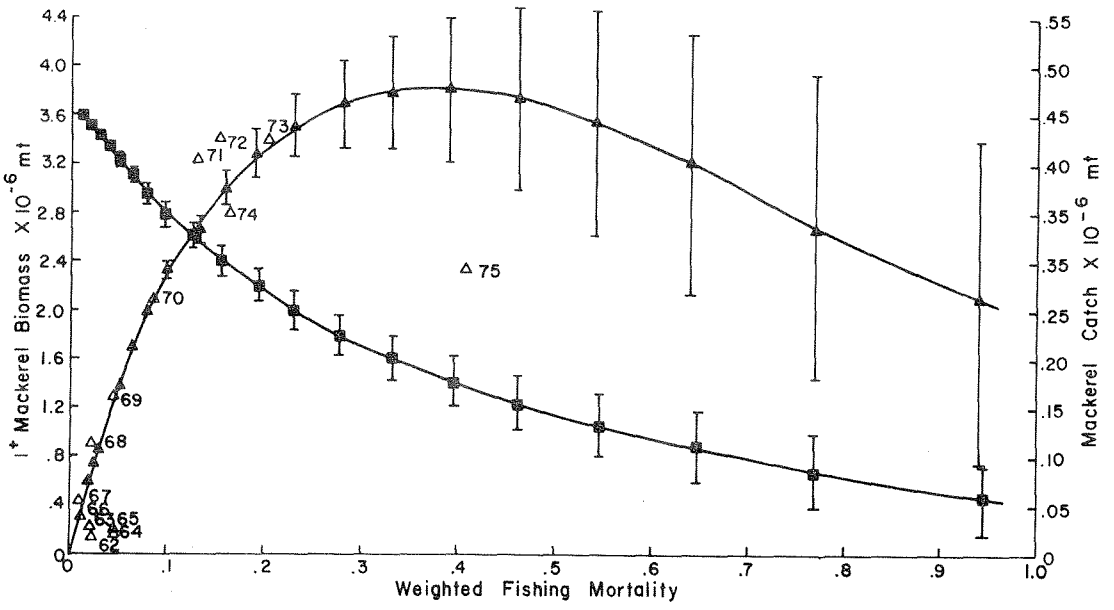

Fig. 24. Relationship between mackerel catch and biomass, for different levels of fishing mortality. Mackerel catches and biomasses have been reduced by 15% from simulated values to represent the fishery in ICNAF Subareas 5 and 6. Bars are ±1 SD. (Biomass ■, catch ▲).

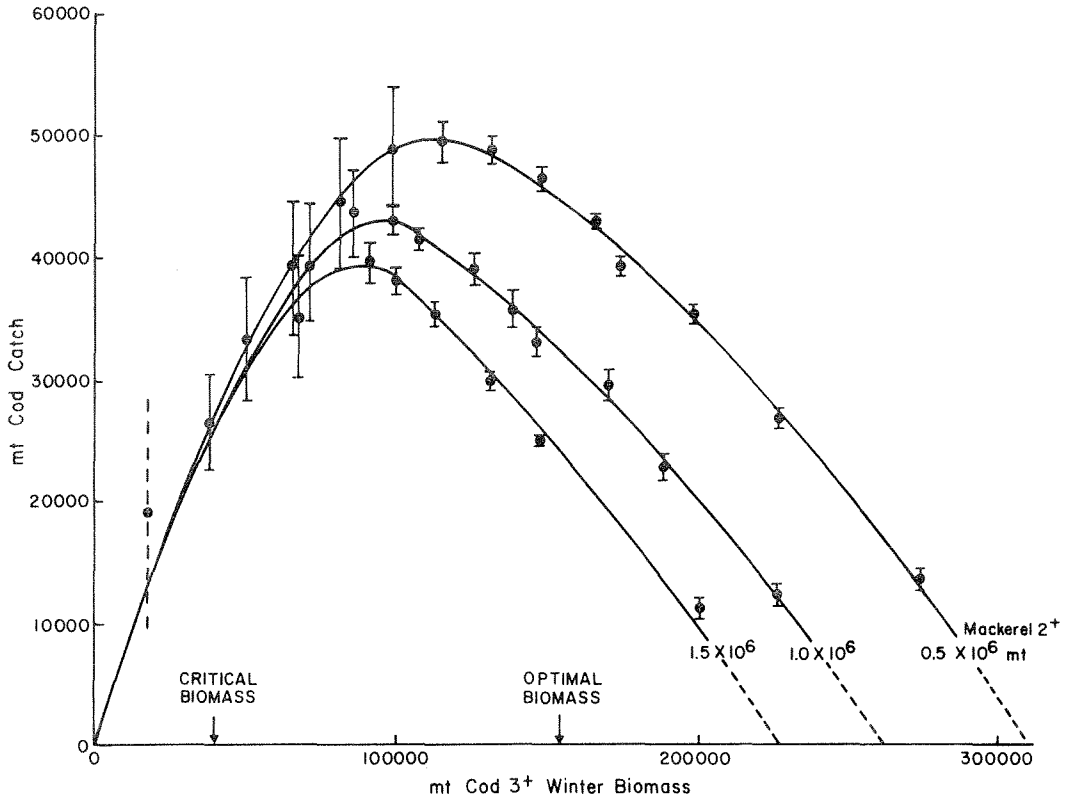

Fig. 25. Relationship between catch and biomass of cod at three different levels of mackerel biomass.

APPENDIX 1

ESTIMATES OF ERRORS ASSOCIATED WITH THE DETERMINATION OF THE ABUNDANCE OF MACKEREL EGGS

One of the major problems associated with the analysis of mackerel egg abundance presented was the determination of the mean and standard deviation of the spawning cycle. Points were determined from cruises occurring in 1967, 1968, 1969, 1977, and 1978. In total, there were 11 points, spread over the ascending and descending limits of the curve,

$$Eg = \beta_0 \exp(\beta_1 T - \beta_2 T^2)$$

where Eg is the abundance of eggs in the total Gulf of St. Lawrence and T is the time in days when the cruise occurred. β_0, β_1, and β_2 are fitted constants.

The parameter values due to a least squares fit were as follows,

$$\beta_0 = 0$$

$$\beta_1 = 2.853$$

$$\beta_2 = -0.008$$

with a multiple correlation coefficient of 0.89 significant at $P \leq 0.01$. In addition, because of the good fit of the curve, it can be concluded that the spawning cycle is approximately standard normal.

Errors due to sampling eggs were then investigated. The major components of this error were associated with splitting, sorting, and counting samples. At the 5% confidence level the standard deviation is on average 16% of the mean egg abundance level.

No estimate could be made for the error associated with the mean day of spawning from our data; however, Ware (pers. comm.) has indicated that in his study all peak spawning dates correspond with a water temperature of approximately 12°C. This implies that mean day of spawning should vary by less than 2 d when corrected for by temperature. It has already been stated that the error in the standard deviation is no more than 2 d.

A sensitivity analysis was conducted in the following manner: The correct estimate of the mean cruise date was assumed to be 27 d. Peak spawning was assumed to occur on day 25. When 29 d was estimated as the mean cruise date the estimated number of eggs increased by 22%. When the mean day of cruise was underestimated by 2 d the estimate of the total number of eggs dropped by 16%. Thus when moving toward the peak of the spawning cycle, underestimates of mean cruise date result in less error in estimate of the number of eggs than overestimates of the mean cruise date.

Next the effect of an error in the estimate of the total number of eggs was investigated. An estimate of the standard deviation at the 95% confidence level was ±16%. On day 27, with a peak spawning date of 25, an error of +16% in the abundance of eggs would result in an error of +16% in the total abundance of eggs during the spawning cycle and vice versa. Therefore, the errors were associated with the estimate of the overall spawning potential.

Errors associated with under- or overestimating the mean date of spawning have that same effect as under- or overestimating the mean cruise date.