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Recruitment: a problem of multispecies interaction and environmental perturbation, with special reference to Gulf of St. Lawrence herring (Clupea harengus L.)

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Abstract

A stochastic model has been developed to study the effects of temperature perturbations, and predation and competition from mackerel (Scomber scombrus) on the recruitment process for Gulf of St. Lawrence Atlantic herring (Clupea harengus). Multivariate statistics were used to determine the structural equation for portions of the life history of herring. It was determined that temperature and the abundance of age group 0 mackerel effected the growth rate of herring, but that neither the total herring biomass or total pelagic biomass had any measurable effect on growth rate of herring. The growth rate of herring, coupled with adult stock size and environmental effects mediated through temperature, where the prime determinants of the abundance of larvae <10 mm. Density dependent growth was found in the l_1 stage, but is argued as being anomolous in relation to age group 0 herring maximizing their production to simultaneously stabilize both 1, and year-class size. Predation, tempered by the available food density is discussed as a major population stabilizing mechanism and a fine tuning mechanism for year-class formation. The ramifications of variation in recruitment are discussed in relation to the Beverton and Holt dynamic pool model and the Shaeffer logistic model. In addition, the Ricker recruitment curve is confirmed as being a viable fisheries management tool.

Introduction

For many years fisheries biologists have studied different portions of the life history of fish in order to determine which is the most responsible for explaining changes in abundance. Ricker's (1954) paper on stock and recruitment was a turning point in the understanding of the problem. He indicated a promising avenue of attack in addition to elucidating the mechanism for modelling the recruitment process. The uniqueness of the approach taken by Ricker is illustrated by the fact that his paper is more important today for its creative and scientific content than for its historical interest. He suggested that recruitment was a continuum, initiated by the adult stocks fecundity then mediated through interspecific competition and subsequent cannibalism by the parent stock. Most other theoretical contributions to the interrelationship between spawning stock and recruitment do not incorporate the effect of environmental variables (Beverton and Holt 1957; Beverton 1962; Cushing and Harris 1973). Notable exceptions are the works of Postuma (1971) and Postuma and Zijlstra (1974). They demonstrated some clear relationships between temperature, herring (*Clupea harengus* L.) larval abundance, and year-class size. Blaxter (1956) and Alderdice and Valsen's (1971) research supports the view of Postuma and Zijlstra by showing that egg survival is related to the environmental effects of temperature and salinity. The accumulation of egg layers on the ocean floor, producing local oxygen minimums and the concentration of predators, (Galkina 1971) have also been hypothesized as extrinsic population control mechanisms. However, it has been suggested by Runnstrøm (1942) and Parrish et al. (1959) that only rarely would egg sheets be detrimentally thick for Atlantic herring.

The distribution of fish larvae in the sea has been investigated for some time (Sette 1943; Ahlstrom 1954; Cushing and Harris 1973; Harding and Talbot 1973; Smith 1973) and is an avenue which shows promise toward elucidating some factors effecting recruitment. Cushing (1975a), Jones (1973), Jones and Hall (1974) and Ware (1975b) have presented particularly interesting models which couple year-class size with larval food density. Of these paradigms, Ware's is the most useful since it demonstrates how growth dependent mortality of eggs and larvae can fit within global ecological principles (Sheldon et al. 1973; Kerr 1974). In addition, his hypothesis incorporates environmental effects mediated through temperature. Lasker's (1975) model is also provocative, relating the initiation of larval feeding to chlorophyll concentrations and large scale hydrographic changes.

The study of the recruitment process requires a well delineated parent stock. For this purpose we have chosen a herring population made up of both spring and fall spawners (Day 1957), which resides mainly in the southern Gulf of St.

Lawrence and off southwest Newfoundland (Fig. 1). The migration patterns of this stock have been investigated by tagging studies (Winters MS 1975).

This population supports a winter fishery along southwest Newfoundland, which migrates across to the Magdalen Shallows some time in May, where the spring component spawns. At this time the stock breaks up with a portion entering the southern Gulf of St. Lawrence and another migrating to the American Bank area which is a major feeding ground for herring (Iles and Tibbo 1970). Historically, this area supported one of the major herring purse seine fisheries, however the emphasis is now on the herring as they migrate over the Laurentian Channel. By July, this northern stock component is dispersed around the Gaspé-Chaleur Bay area where an extensive spawning occurs in late summer and early autumn. In October-November the stock emigrates from the southern Gulf of St. Lawrence back to southwest Newfoundland. During the summer months this herring stock interacts with a mackerel (Scomber scombrug) stock that migrates into the Gulf of St. Lawrence from the Scotian Shelf and Gulf of Maine area (Moores et al. 1975).

It is the purpose of this paper to present a stochastic model which amalgamates the recruitment process with the general dynamic pool fisheries models of Parrish and Jones (1953), Beverton and Holt (1957), and Ricker (1958) to elucidate the long-term effects of fishing as well as investigate the concept of equilibrium yield. The simulation can be termed multispecies, since it includes the effects of both herring and mackerel on the recruitment process for herring. In addition, temperature is incorporated since it is considered to be the key environmental factor affecting recruitment. Methods

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In 1965 an investigation of the distribution and abundance of fish eggs and larvae in the southern Gulf of St. Lawrence was initiated and subsequently continued until 1975. However, it was only in 1967 that the cruises were designed to concentrate on herring larvae in addition to other larval species. For the present analysis, only the samples from three types of nets were considered, standard conical and meter nets, Miller samplers and 61-cm bongo nets (Kohler et al. 1974). The conical nets were 3.2 m long and were constructed of No. 471 Nitrex nylon. The Miller samplers were constructed from plans made available by NOAA, Woods Hole, Mass. This gear type, with a mouth diameter of 10.8 cm, was smaller than the meter nets and bongos.

Volumes of water strained by the standard conical meter nets were measured with TSK flow-meters (Tsurumi-Seiki Kosakusho Co. Ltd., Yokohama, Japan). The meter nets were stacked on a towing wire at the surface and 15 m depths. The Miller samplers towed in a similar manner were positioned at 5-m intervals from surface to 40 m, while the bongos were towed in pairs at 10-m depth intervals. The towing speed was 2 1/2 knots for 30 min. All depths were not towed simultaneously resulting in the station position being confounded with depth. The ships used for these cruises were the M.V. Harengus, C.G.S. E. E. Prince and A. T. Cameron. (Cruise dates used for this analysis appear in Appendix I).

The nets were thoroughly washed down with salt water when brought aboard after towing. Samples were routinely stored in 0.95-*l* glass bottles in 10% formalin. Larval fish were separated and identified by species. Large samples were subsampled using a 'Falsom plankton splitter'. The samples or subsamples were spread in large flat trays with a black background and examined under reflected light by a microscope or magnifying glass. The herring larvae were subsequently separated individually and counted. A more detailed description of length frequencies, distribution patterns and drift speeds is given by Messieh and Kohler (1972).

Before an analysis was possible, some amalgamation of the large amounts of data collected between 1967 and 1972 was necessary. The strong autocorrelation between successive tows within a cruise, due to the aggregation of larvae, suggested the best method to observe unbiased patterns within the data was to treat the entire cruise as one experimental unit. The analysis of the data could then be treated as a multiple split plot design (Cochran and Cox 1968) with cruises being the main plot. The first split within cruises was a breakdown of gear types, all adjusted to a constant amount of water strained (100,000 m³). Those with a different mesh size than No. 471 Nitrex in the codend were not used in the analysis. Calculated flows on the meter nets did not differ from the observed flows taken by the TSK flow-meters by more than 5%. This level of accuracy was assumed to apply to the calculated flows for other nets.

Preliminary analysis of the gear types showed that adjusted herring larvae catch/100,000 m³ for Miller samplers, Bongos and 1-m nets were not significantly different. Catches in the other gear types were an order of magnitude lower than these, and were not comparable. In addition, the length frequencies of larvae caught in these gear types were not significantly different, whereas the neuston and Issacs-Kidd trawl tend to catch much larger larvae.

The next split within gear was depth. Depth was not found to be significant in determining larval availability. The uniformity of larval catches over depth possibly has no biological

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significance and may be a result of the confounding of depth and position.

Response surface techniques (Cochran and Cox 1968) were used to determine the relationship among the dependent and independent variables. The fitting procedure employed either a linear polynomial

$$x = b_0 x_0 + b_1 x_1 + b_2 x_2 + b_{11} x_1^2 + b_{22} x_2^2 + b_{12} x_1 x_2$$

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

The biological basis of the model

Factors regulating the growth rate

The instantaneous growth rate of herring age groups 2-10 was defined as, $G = \frac{dL}{dtL}$, and calculated from length at age data of Messieh (MS 1973) and Winters (MS 1975). Samples of these two studies were collected at different times and localities, but as they were from the same stock, the growth rates were considered comparable, since the times between sampling remained consistent.

Age-groups, Y_a, rather than ages were used as the

stock contained both spring and fall spawners. Thus, a fish was placed in age-group 0 in the year of its birth, regardless of whether it was spawned in the spring or autumn, and both types enter the next age group at the same time the following year. To maintain some consistency of age-group designation throughout the fishery year, a cohort was considered to enter an age-group at the start of the fishery year in April (Winters and Hodder 1975).

To elucidate the factors regulating the growth rate, the data was analysed using stepwise multiple regression. The following intrinsically linear model adequately described the growth of herring:

(1)
$$\log_e G_a = -4.701 \log_e Y_a - 0.161 \log_e M_y + 0.827 \log_e Y_a \times \log_e T_m + 6.028$$

where the independent variable M_v is the year-class size of age

group 0 mackerel x 10^{-6} . It is assumed that the entire Atlantic mackerel stock migrates into the Gulf of St. Lawrence during the summer months since there are no absolute estimates to indicate otherwise. However, this assumption is not critical since all variables in the equations associated with mackerel would be scale accordingly. T_m is the annual, mean, monthly

maximum temperature at Grande Riviere in degrees celsius. Grand Riviere is on the western shore of the southern Gulf of St. Lawrence, and the temperatures at this location are well correlated with the cruise temperatures (Lett et al. 1975a).

<u>Variable</u>	Coeff.	<u>S.</u> E.
log _e Y _a	-4.701	1.110
log _e M _y	-0.161	0.056
log Y _a x log T _m	-0.827	0.427

The coefficient of multiple determination (R^2) is 0.89 while the F value for regression is 231.0¹ (F'_{3,87}/2.70). (See Appendix IIa for the correlation matrix).

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Cohort analysis (Pope 1972) was used to determine the numbers at age one and older from catch at age data (Anderson . 1975). The abundance of age group 0 mackerel was calculated by projecting back the numbers at age group 1, using a natural mortality rate of 0.3 (ICNAF Summ. Doc. 1975). The year-class sizes prior to 1968 were calculated by projecting the 1968 population structure back, assuming the same natural mortality rate. The fishing mortality was held at zero, as there was virtually no fishery for mackerel during the period between the epizootic disease in the mid 50's and 1966. Therefore, a projection back to 1959 was assumed to give a reasonable account of the changes in recruitment.

It has been hypothesized that there is a difference in the growth rate of spring and fall spawners (Day 1957). Since this variable does not take on values over a continuous range, a dummy variable (Draper and Smith 1966) was added to the analysis. The variable was not found to be significant, and we concluded that there were no differences in the growth rates.

Furthermore, preliminary analysis indicated that the growth rate of herring was unrelated to its biomass. This analysis included data from 1959 to 1972, a time interval in which the stock transformed from its lowest recorded biomass to its highest during the 60's, and subsequently during the 70's declined to levels of about 1/4 the maximum. The failure of 1+ herring to show density-dependent growth is common to most stocks that have been studied (Burd 1962; Cushing 1975). This appears ecologically sound (Kerr 1974; Sheldon et al. 1973), as herring feed on small particles with a high turnover rate, and a severe depletion of a standing stock of zooplankton through excessive grazing seems implausible. In fact, Brett (1971) shows the young pelagic feeding salmon will terminate their foraging as soon as it becomes an energetic disadvantage.

Growth rate also declines rapidly in response to an increase in the size of the 0-group mackerel year-class (Fig. 2), the decline at low abundance levels being much more rapid than at higher abundance levels. This rapid response may be explained by the high growth rate of juvenile mackerel (12.5%/day in wt, Royce 1972) which feed on the same standing stock of plankton as the 1+ herring. However, when the mackerel return to the Gulf of St. Lawrence (Moores et al. 1975) in their second year of life, they have moved onto larger food particles and compete with the herring very little (D.M. Ware, personal communication). The failure of the overall mackerel biomass to significantly explain changes in the herring growth supports this observation.

Temperature was found to interact significantly with the age variable which is an index of herring size, at least in the younger fish. This interaction was positive, suggesting

¹Significant at P<0.05

that temperature increased the instantaneous growth rate of larger herring more than the smaller ones, possibly because the basal cost per unit weight of the larger fish is less (Beamish 1964). The interaction was also weak, which is demonstrated by the low ratio of the coefficient to standard error, presumably because fish will select temperatures which are optimal for growth (Brett 1971).

The rapid decline in herring growth rate with age (Fig. 2) is reflected in the early attainment of asymptotic length. An exponential decline in the instantaneous change in length is coupled with an acceleration and subsequent deceleration in the instantaneous growth rate with weight, the inflection point being near the onset of maturation. Since growth and mortality are not independent (Cushing 1975b; Ware 1975b) it might be argued that the rate of formation of high energy gonadal products, especially after the achievement of asymptotic growth, is a balancing force which responds to the mortality rate. If the preceding arguement is true, the larval production of herring should be reflected by their growth rate.

Factors regulating larval production

There are numerous examples of a positive correlation between "spawning potential" and the abundance of herring larvae (Cushing and Bridges 1966; Burd and Purnell 1973; Postuma and Zijlstra 1974; Saville et al. 1974). Spawning potential usually is an index or a calculation of the adult stock biomass. Nevertheless, these correlations are not that good, and usually never explain more than 60% of the variation in larval abundance (Postuma and Zijlstra 1974).

An additional portion of the variation may be explained by adding a variable related to the total annual energy intake of the adult stock. Normally, the growth rate reflects food availability (Parrish 1975) and therefore can be used as an index of the amount of energy partitioned into gonadal products. Recently, Lett et al. (1975a) found that the abundance of pelagic cod eggs was related to the growth rate and temperature. This result is expected since Scott (1962) and Tyler and Dunn (1976), in laboratory experiments, have clearly shown that realised fecundity depends on the number of maturing follicles undergoing atresia, and the degree of atresia is related to the ration size. Nikolsky (1969) and Bagenal (1966) have hypothesized that ration size, by modifying fecundity, is indeed a population control for teleosts.

There is no published evidence that ration or growth are correlated with the fecundity of herring, yet the evidence from other species clearly suggests that egg production is related to the production of the adult stock, defined as N Δw . To test this hypothesis, the production of the adult stock was calculated for both the spring and fall spawning populations using the equation:

$$\begin{array}{ccc} a=8\\ (2) & P=\sum_{a=2}^{a=8} & N_a \times E_a \times G_a \end{array}$$

where N_a is the numbers at age a, calculated by cohort analysis

(Winters and Hodder 1975). Only the age groups 2 to 8 were used, since there were very few animals older than 8 making an estimation of these numbers unreliable. G_a is the instantaneous growth rate calculated from equation (1). The instantaneous growth rate was used since E_a , the maturity, is merely

an index of the average length of herring in a cohort. The maturity ogives for spring and fall spawners are fixed, intrinsically linear functions of length (Messieh 1976).

Postuma (1971) and Postuma and Zijlstra (1974) have indicated an additional proportion of the variation in larval abundance may be explained by changes in temperature. For this reason, both temperature and the production of the adult stock were considered to be variables of importance and were included in the following equation:

(3) $L_R = -5.700 P + 1.804 T_p x P - 0.097 T_p^2 x P - 0.656$

Variable	Coeff.	<u>s. e.</u>
Р	-5.700	1.934
т _р хР	1.804	0.394
T _D ² x P	0.097	0.019

The coefficient of multiple determination (R^2) is 0.98 while the F for regression is 126.8² (F'_{3,6}/8.94). (The correlation matrix is in Appendix IIB).

The temperature variable T_p is the temperature at

Grande Riviere during the mid point of the larval cruise. For the spring spawners this was sometime in May and for fall spawners August, except in 1967 when there were no larvae <10 mm until October. The August and September temperatures in this year were excessively high and may have delayed spawning. Both the spring and fall spawned larvae, $L_p/100,000 \text{ m}^3$, are considered as separate data points and the validity of the treatment of the data seems to be justified by the goodness of fit of the relationship.

The abundance of spring spawned larvae is positively correlated with temperature while the abundance of fall spawned larvae is negatively correlated, a fact which is documented for the North Sea stocks by Postuma (1971). As Postuma and Zijlstra (1974) have more recently pointed out, the relationship of temperature to egg and larval survival is probably quadratic with an optimum. Blaxter (1956) has demonstrated that there is an optimum temperature for herring egg survival; however, the biological basis of the quadratic effect of temperature in equation (3) is not clear, since the effect could be mediated through the eggs or the larvae, or the larval food supply, or any combination.

The relationship between the annual abundance of larvae <10 mm and herring production, with temperature effects removed is displayed in Fig. 3. Messieh (1976) has shown that the fecundity of fall spawners is greater than spring spawners. Apparently, spring-spawned eggs are about twice the size of the more numerous fall-spawned eggs, and this fact may contribute

²Significant at P<0.05

to the greater abundance of fall larvae. However, our hypothesis would relate the high densities of fall larvae to a greater biomass of the fall stock (Winters and Hodder 1975) if growth rates were the same for both spring and fall spawning fish. As a compensation for their lower fecundity, spring spawners mature at a smaller size and it is quite possible that if the stock sizes for both fall and spring spawners were equal, then so would be their respective contributions to overall egg production. The earlier maturation of the spring spawners, then, is possibly an adaptive control mechanism to compensate for the larger eggs they must produce to deal with more adverse environmental conditions (Hempel 1965; Ware 1975b).

Factors effecting year-class formation

According to Burd's (1962) hypothesis, the length of herring at the end of the first year of life (l_1) results in

marked length differences later in life. It could be argued that if 1+ herring growth is not density dependent, the stock has no capacity to adjust its biomass on a short-term basis (Lett and Doubleday 1976). Therefore, the only natural means for regulating a stock on a long-term basis is through fecundity, with the time of maturation being related to the l_1 size.

Density-dependent growth for 0-group clupeids has been well established for herring and Pacific sardines (*Sardinaps caerulea*) by Iles (1967, 1973). Using l_1 's back calculated from herring scales by Messieh (MS 1973), we have also established a density dependent growth relationship with yearclass size for Gulf of St. Lawrence herring (Fig. 4). The following equation represents the relationship:

(4)
$$\ell_1 = 4.252 \times 10^{-9} Y_R - 2.768 \times 10^1 D + 168.71$$
 $R^2 = 0.73$
 $F = 19.16^3$

where l_1 is the length in mm, Y_R is the size of the year-class

at age 2 and D is a dummy variable (Draper and Smith 1966) representing the difference between spring and fall spawners. Both spring and fall spawning herring are combined to represent the year-class size since they are assumed to compete during the overwintering period and spring in their first year of life. Although juvenile herring have been found in a number of localities in the Gulf, it is assumed that the major portion of the 0-group fish school in the mouth of the St. Lawrence River.

The size of the presnet year-class is reflected in the density-dependent l_1 growth, and since maturity is a fixed

function of length, future year-class sizes are related to the present one. For example, the age of 50% maturity has varied by as much as 2 yr for this stock in response to variations in l_1 . It would follow that depending on the length

at age, there can be a dramatic difference in the gonadal production of equally sized cohorts. Thus individual fish in a less abundant cohort mature sconer and may produce more gonad in their lifetime than fish in a more abundant cohort. In this way, the overall egg production of two unequally sized stocks can remain relatively equivalent, thus rendering the longterm biomass of the stock equal. However, this inherent stability is shaken by the variable effects of temperature and the size

³Significant at P<0.05

of the age group 0 mackerel year-class on herring growth (see equation 1). Information on the size of the present spawning population, stored by their progeny, will be partially destroyed by temperature and competitive perturbations before it is released into subsequent generations. The offsetting of the optimal maturity schedule, by a random environment, indicates herring must have a more precise homeostatic control mechanism than has been suggested so far.

As illustrated for the Pacific sardine (Lett and Doubleday 1976) and for Gulf of St. Lawrence herring (Fig. 4), there is a central tendency of year-class size and l_1 length. This tendency of cohorts towards a constant l_1 is implied by

Ware (1975b) in relation to the dependence of mortality on the growth rate of juvenile fish. We also wish to suggest that it is only under unusual conditions that l_1 will vary enough

to make density-dependent growth observable. A good example of an atypical condition would be the ensuing catastrophic population changes that developed in the wake of the epizootic disease in the Gulf of St. Lawrence. At this time, the herring and mackerel stocks were severely depleted (Sinderman 1958), reducing the predatory pressure on herring larvae.

The scenario for this central tendency towards maximization of production is as follows (Fig. 4). Pelagic fish seem to have an optimal swimming speed associated with the food concentration of their prey organisms which serves to maximize their growth rate (Weihs 1973; Ware 1975a). If a fish population is simultaneously trying to maximize survival and growth rates, then production,

 $\mathbf{P} = \mathbf{N} \Delta \mathbf{W}$

will also be maximized such that

(5) $dP = dN \cdot \Delta W + N \cdot d(\Delta W) = 0$

and by rearrangement of the terms results in

$$(6) \quad \frac{-\mathrm{dN}}{\mathrm{N}} = \frac{\mathrm{d}(\Delta W)}{\Delta W}$$

which simply means that the mortality rate is equal to the instantaneous acceleration of growth. Using a simulation, Lett (unpublished data) has investigated the implication of this equation as a predatory process. Growth accelerates as larvae begin cropping down the standing crop of phytoplankton that are in close enough proximity such that predation is not at an energetic disadvantage. However, as food becomes scarce, starvation begins and growth decelerates since larvae are not efficient enough swimmers to move onto a new foraging location when the local standing crop becomes depleted. Predation by 1+ herring and mackerel (unpublished stomach content data, B.S. Muir, personal communication) is assumed to result in the selection of the weaker larvae which are unable to avoid them. This allows the surviving larvae's food supply to build up once more. The acceleration of growth is coupled to the predatory rate, i.e., mortality rate, since the degree of overcropping is determined by the accelerated growth phase, and will subsequently regulate the rate of starvation. The higher the predatory rate, the faster that the starving larvae are removed from the system. However, accelerated growth of the remaining larvae cannot resume until the food supply has had time to build up once more. Assuming that predators are only efficient at capturing weakened larvae, the time to the next sequence of starvation is unrelated to the predatory rate in the present

starvation sequence. Therefore, the only noticeable difference in larval abundance that should be mediated through predation, occurs when the predatory rate on larvae is low enough to prevent the buildup of the local phytoplankton populations. Since even poorly conditioned larvae will capture food, and phytoplankton increases exponentially, only a very nominal level of larval predation can keep the phytoplankton in a depleted state. It is interesting to note that after a given number of days of starvation herring larvae will lose their ability to eat (Hempel 1965), and from a competitive point of view may be considered as dead. This provides a possible adaptive mechanism allowing the remaining larvae to grow. Although these surviving larvae will ultimately be smaller at metamorphosis, the numbers surviving should be greater. In summary, year-class size and the weight at the end of the first year of life respond exponentially to predation. This exponential response may only be a mathematical interpretation of a much more discrete event. Furthermore, all other factors being constant, the main forcing function is food density. An obser-vation of these events on a larger scale would also be masked by the heterogeneities of plankton patchiness.

If the former argument is true, year-class size should be related to the number of larvae and the total pelagic biomass, $B_{TP} \times 10^{-6}$, (Winters MS 1975) made up of 1+ herring and mackerel.

Although there are other pelagic species, herring and mackerel by far make up most of this biomass.

This hypothesis was tested using multiple regression analysis. The following equation, forced through the origin, was used to test the relationship:

(6) $\log_{e} Y_{R} = 2.679 \log_{e} L_{R} - 5.000 \times 10^{-5} [\log_{e} L_{R}]^{2} \times B$ - 0.165 $[\log_{e} L_{R}]^{2}$

Variable	<u>Coeff.</u>	S.E.
log _e L _R	2.679	4.350 x 10 ⁻¹
[log _e L _R] ² x B _{TP}	5.000×10^{-5}	1.543 x 10 ⁻⁵
[log _e L _R] ²	-1.652×10^{-1}	7.400 x 10^{-2}

The coefficient of multiple determination (R^2) is 0.88 while F for regression is 26.25^4 (F'_{3,11}/3.98) (the correlation matrix is in Appendix IIC). Y_R is the addition of both the spring and fall year-class sizes x 10⁻⁶, determined by cohort analysis (Winters and Hodder 1975) from 1965 to 1971. The year-class sizes from 1959 to 1964 were calculated by projecting the 1965 population structure back assuming a natural mortality of 0.2 (Winters and Hodder 1975) and a fishing mortality which corresponded to the effort and partial recruitment in the appropriate year and cohort (Winters, personal communication).

The number of larvae/100,000 m^3 , L_R, of water was predicted by equation (3), using the calculated production in

⁴Significant at P<0.05

individual years between 1959 and 1971 and to the sea surface temperature from Grande Rivière corresponding to the midpoint of all spring and fall cruises, which comprised temperatures on May 20 for spring spawners and August 25 for fall spawners.

The year-class size increases very abruptly when the total pelagic biomass falls below 109 metric tons (Fig. 5). To draw the graph in this area is unrealistic since a low pelagic biomass would result in a scarcity of larvae, and therefore only the back corner of the response is shown. As the herring biomass increases, year-class size cuts a diagonal slice through the response, with variations on either side of a deterministic path resulting from stochastic environmental and systematic predatory perturbations. It is this diagonal slice through the larval, pelagic biomass plane which produces the Ricker (1954) stock recruitment curve.

Ricker (1954) originally postulated that predation was the fine tuning mechanism for the recruitment of salmon, and Lett et al. (1975a) have hypothesized a similar effect for cod. It follows that predation by mackerel and cannibalism by older herring would be the ultimate population control on juvenile herring, allowing for the maximization of production, giving the optimal trade-off between fish size and numbers. The result is population stability.

Simulation technique

A simulation was constructed combining the structural equations of the early life history of herring to those encompassing current fisheries theory (Parrish and Jones 1953; Beverton and Holt 1957; Ricker 1958). Each of the derived equations seemed to have a firm biological basis in addition to being statistically significant. The objective of the simulation was to study the emergent properties (Kerr 1974), and their relationship to fisheries management.

The program, written in APL, is represented by the schematic flow chart in Fig. 6. The program can be executed with a submodel representing a mackerel fishery, which runs independently of the simulated herring fishery, and generates annual mackerel biomasses and age group 0 year-class sizes. The mackerel biomass generator is a sine wave around a mean biomass with a given periodicity and stochastically varying amplitude. Yearclass sizes of mackerel are determined by the mackerel biomass and a random normal temperature variable in relation to the structural equations presented by Lett et al. (1975b).

However, when it is desirable to control the mackerel biomass and year-class size to study the system more closely, the program can be initialized by entering the mackerel biomass

x 10^{-6} , the size of the juvenile mackerel year-class, x 10^{-6} , the numbers at age for spring and fall spawners, for ages 1 to 16, the fishing mortality for spring and fall spawners and the number of years the simulation is to run. Since the initial weights at age for spring and fall spawners, and the selection at age for spring and fall spawners, will not vary from run to run, they were initialized as fixed vectors. However, after each iteration of the simulation, the abundance of spring and fall spawners and the weights at age vectors will be recalculated internally within the simulation model.

The main program, representing the herring fishery, begins with an internal clock which is annually updated by each iteration. To calculate yield for both the spring and fall fisheries, the standard catch equation (Beverton and Holt 1957) with an annual natural mortality, M, of 0.2 (Winters and Hodder 1975) was used:

$$Y = \sum_{a=1}^{a=16} \frac{N_a W_a \partial_a F(1-EXP(-(\partial_a F + 0.2)))}{\partial_a F + 0.2} I$$

where F is the fishing mortality, ϑ_a is the selection at age and N_a and W_a are the numbers and weights at age. The catches are accumulated into a vector of the same length as the number of years being simulated.

Following the calculation of catch the remaining biomass is calculated by the equation:

$$B = \sum_{a=1}^{a=16} N_a W_a EXP(-(\partial_a F + 0.2))$$
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for both spring and fall spawning herring. These values are also accumulated for the length of time the simulation will run.

The next stage in the program is to calculate the instantaneous growth rate which is a function of the age group 0 mackerel year-class size, M_v , and temperature, T_m .

Temperature is the annual, mean, monthly maximum and is considered to be a normal deviate with mean 14.39 and deviation 1.11, based on observed sea surface temperatures at Grande Riviere. The following equation is used for both spring and fall spawners:

$$\log_{e}G = -4.071 \log_{e}Y_{a} \sim 0.161 \times \log_{e}M_{y} + 0.827 \log_{e}Y_{a} \times \log_{e}T_{p} + 6.0283$$
 III

The growth rate x 10^2 is determined from the exponent of G.

The weights at age, W_a , of spring and fall spawning

herring are now converted to lengths L by the formulae

$$L_{a} = \begin{bmatrix} \frac{W_{a} \times 10^{5}}{2.55} \end{bmatrix} \begin{array}{c} 0.3005 \\ \text{for spring spawners,} & \text{IV} \end{bmatrix}$$
$$L_{a} = \begin{bmatrix} \frac{W_{a} \times 10^{5}}{9.72} \end{bmatrix} \begin{array}{c} 0.3445 \\ \text{for fall spawners.} & \text{V} \end{bmatrix}$$

Using the lengths at age for spring and fall spawners, the fraction mature at age, E_a , is determined by:

ARC SINE $E_a = 9.769L_a - 245.2$ for spring spawners VI

anđ

ARC SINE
$$E_a = 8.011L_a - 204.6$$
 for fall spawners. VII

The ARC SINE of E_a is constrained such that it cannot be >90 or <0.

Using the combination of the numbers at age, maturity, and instantaneous growth rate, the production, P, of the spring and fall stocks for ages 2-8 is calculated by the formula:

This production, coupled with a spring and fall sea surface temperature at Grande Riviere, T_p, of means 5.37 and 12.25

with standard normal deviations of 1.21 and 3.13 respectively were used to calculate the numbers of spring and fall larvae <10 mm produced by the stock. The equation used for this purpose was:

$$L_{R} = -5.700 P + 1.804T_{p} \times P - 0.097T_{p}^{2} \times P$$
 IX

and the numbers of spring and fall larvae were summed to produce the total number that results in a combined year-class size.

The total pelagic biomass $B_{TP} \propto 10^{-6}$ is also important in determining year-class size, $Y_R \propto 10^{-6}$, since these herring and mackerel predate on herring larvae. The equation describing this event is:

$$\log_{e} Y_{R} = 2.679 \log_{e} L_{R} - 5.000 \times 10^{-5} [\log_{e} L_{R}]^{2}$$
$$\times B_{TP} - 0.165 \times [\log_{e} L_{R}]^{2} \qquad X$$

The year-class is then broken up into spring and fall spawners by multiplying by the ratio of spring and fall larvae to the total number of larvae.

Using the year-class size, $Y_R \propto 10^{-6}$, the length of herring at the end of the first year of life, l_1 , is determined by the following equation:

$$\ell_1 = -0.00425 \times \mathrm{Y}_\mathrm{R} + 141.8$$
 for spring spawners $~\mathrm{XI}$ and

 $\ell_1 = -0.00425 \times Y_R + 168.7$ for fall spawners. XII

These lengths are converted to weights using the following expression determined for juvenile herring:

$$W_1 = 3.5 \times 10^{-6} \ell_1^{3.11}$$
 XIII

with this weight being converted to kilograms by dividing by 1000.

The numbers at age are now updated by the formula:

$$N_{a+1} = N_a EXP(-(F + M))$$
 XIV

and the juvenile cohort is catenated into the position in the vector for 1-year-olds after being multiplied by 1.22 x 10^6 since Y_R is the year-class size at age two. The remaining

herring that are now 16+ are dropped from the vector. The lengths at age are now updated by multiplying by the growth rate G_a (equation III) such that:

$$W_{a+1} = W_a EXP G_a$$
 XV

The lengths are now converted to weights using the expression:

$$W_a = 0.00255 L_a^{3.328}$$
 XVI

for spring spawning herring and

$$W_a = 0.00972 L_a^{2.903}$$
 for fall spawning herring. XVII

The l_1 herring are now catenated into the position in the vector for 1-year-old herring and the weight for the 16+ herring is dropped from the vector.

A test is now made to see if the simulation period has expired, if not, the program returns to start and updates the internal clock by one year. Otherwise, a data matrix is printed out and the graphic subroutines executed.

Results and discussion of the simulation

The simulation was run for 100 yr starting with the 1965 spring and fall populations determined by cohort analysis. When the mackerel biomass was fixed at values between 2 x 10^6

and 0.5 x 10^6 m.t., the spring and fall population biomasses initially declined for the first 10 yr (Fig. 7). Thereupon, the fall population began a rapid increase and the spring population continued on a slower decline, reaching a minimum level within 70 yr. However, when a fluctuating mackerel biomass was added to the simulation, the spring spawning population no longer collapsed but continued to oscillate at a level of about 2/3 the fall spawning biomass. It appears that the irregular yearclass strengths produced by the oscillating mackerel biomass added robustness to the model. The number of age group 0 mackerel influences the growth rate of adult herring (see equation 1, Fig. 2). When the growth rate is high, during a period of small mackerel year-classes, gonadal production (see equation 2) and subsequent larval production increases. Furthermore, the juvenile 2 and 3-year-old herring reached maturity sooner which resulted in an additional amount of gonadal production which can be attributed to these younger year-classes. Therefore, it was erratic, but strong, year-classes which kept the spring stock viable.

Most herring stocks on the eastern seaboard of North America are fall spawners, although there is a progression toward spring spawners in the more northern limits of their range (Leim 1957). Some insight may be gained from the simulation regarding the preponderance of the fall spawning herring stocks. Both stocks are of comparable abundance at the outset, thus the dominance of the fall spawners must be related to biological factors other than production of the adult stock. Indeed, spring spawners mature at smaller sizes. As stated previously, spring larval abundance was positively correlated with temperature while fall larval abundance was negatively correlated. However, the distribution of fall temperatures in the Gulf of St. Lawrence is in closer proximity to the optimum temperature 9.3°C than the distribution of the spring temperatures. The l_1 length of fall spawning herring

is longer than spring spawning herring, but the greater relative maturity at length of the spring spawners will provide some compensation for this discrepancy. It is observed that the spring herring stock in the Gulf of St. Lawrence is now exiguous, which possibly is the result of overfishing in addition to poor recruitment.

The addition of 10^6 m.t. of mackerel to the Gulf of St. Lawrence means about an equivalent reduction in herring biomass (Fig. 8). The variance in herring stock biomass was much less when it was associated with a fixed mackerel biomass than when mackerel were not included in the simulation. It appears that the affect of mackerel predation resulted in a dampening of the variance in herring larval production.

The trade-off between herring and mackerel is demonstrated more clearly in Fig. 9. The simulated competitive relationship between herring and mackerel indicates that when there are 2 x 10^5 m.t. of mackerel, the herring biomass constitutes 1.5 x 10^6 m.t. for a total pelagic biomass of 1.7 x 10^6 m.t. Yet, when there are 1.50 x 10^6 m.t. of mackerel, herring

make up 5×10^5 m.t. for a total pelagic biomass of 2×10^6 m.t. These numbers tend to indicate that the trade-off is almost equivalent, with herring having a slight advantage over mackerel, even though mackerel are assumed to determine the fate of the herring stock to some extent. In other words, the production of the pelagic fish community of Gulf of St. Lawrence is fixed within narrow limits such that biomass remains relatively constant. This type of concept has been stressed by Dickie (1972) for some time as being an important management consideration.

The reason for this advantage in favour of herring may be the consequence of mackerel only being present in the Gulf from May to October. The close agreement between the simulated and empirical results suggests that much of the decline in herring biomass between 1962 and 1972 may not have been entirely due to overfishing, but rather the result of an increased proliferation of mackerel. Therefore, the management of mackerel may be as important as the direct manipulation of the herring stock in determining the available biomass for exploitation. The trade-offs occurring in Fig. 9 are in response to varying the amount of mackerel predation, while the age group 0 mackerel abundance remained fixed. However, as the mackerel biomass oscillates, so will their year-class sizes (Lett et al. 1975b), and growth rates and maturity of herring have previously been shown to be sensitive to wide fluctuations in the age 0 mackerel cohort. If mackerel is exploited in an optimal manner, the year-class sizes formed will fluctuate around a value

between 3 x 10^9 to 7 x 10^9 fish (Lett et al. 1975). These year-class sizes will suppress the growth of herring to such a degree that late maturation and poor gonadal production causes the Gulf of St. Lawrence herring stock to collapse. Yet, when the mackerel biomass is not exploited, and sustains itself at a higher level with smaller year-class sizes (ranging between

 10^7 and 7 x 10^9 individuals), the herring maintain a viable population of both spring and fall spawners. Thus, the pulsing effect of mackerel seems to produce a greater biomass of herring with more vitality. It is apparent from this study that both herring and mackerel cannot be exploited at an optimal level simultaneously. In fact, in order to maintain a herring fishery in the Gulf of St. Lawrence, it would be better to either over or not exploit mackerel.

This outcome has a firm holistic, ecological foundation. Dickie (1972) has clearly demonstrated that logarithmic units separate the turnover rates on P/B ratios of different trophic levels. When mackerel are not being exploited their turnover rate is equivalent to the natural mortality rate (0.3) assuming their standing crop is being maximized. As they become exploited, there are a greater proportion of younger faster growing fish, presumably due to to productions of larger year-classes. At the optimal exploitation level, the mackerel P/B ratio has risen to 0.9 (Lett et al. 1975). This rate, coupled with the natural mortality of herring (0.2), is greater than the turnover rate of their food supply (approximately 1.0 assuming an ecological efficiency of 0.1) and must result in herring, which are outcompeted, disappearing. However, this reasoning is only valid when the carrying capacity available to the pelagic biomass is being fully exploited, which usually is the case (Fig. 9).

North Sea herring larval production is used as a check on the relative sizes of the parent stocks (Zijlstra 1970). То study the precision of this management technique, the simulated larval production was considered a function of stock biomass (Fig. 10). The larval abundance is indeed some expression of stock size but the associated variance makes it an almost impossible predictive tool. Postuma and Zijlstra (1974) have pre-viously noted that the regression of larval abundance on spawning potential does not pass through the origin. Our results also show the same response, in addition to providing some clues concerning the cause. Larval mortality varies quite dramatically in response to temperature (see equation 3), thus no matter what the adult production, there is a probability of a small year-class. These smaller year-classes result in the regression line going through the ordinate somewhat short of the origin.

The simulated results demonstrate that any estimations of year-class size based on the abundances of larvae less than 10 mm are particularly hazardous. The variability in yearclass size inflates as the larval abundance increases and subsequently declines on the descending limb of the curve (Fig. 11). Thus, predictions of small year-classes based on larval abundance will be much more reliable than predictions of larger year-classes. The end product is a dome-shaped relationship with an enormous variance in year-class size associated with the crest. Theoretically, the dome results from the diagonal transect of year-class size across the larval abundance and total pelagic biomass planes and represents the conjoint increase in larval production and predation by herring and mackerel (Fig. 5). When the stock biomass is low, resulting from exploitation, the points will be on the ascending side, but when the stock biomass is high, the points will be predominately on the descending side and crest.

The variance in year-class size is greatest at the dome since this is the vicinity of larval abundance in which year-class size is most sensitive to changes in pelagic biomass. This is especially true when the mackerel biomass is oscillating independently of the herring biomass, a fact which produces a sizeable variance when these two species interact. At larval abundances below and above the area of the dome the year-class formation becomes increasingly less responsive to variations in pelagic biomass.

Year-class size should tend toward some central area such that an equilibrium can be struck between recruitment and mortality (Fig. 4). When there are surplus larvae resulting from a large adult stock, the result is a smaller than average year-class in reply to overcropping by the stock which produced them. The smaller year-classes lead to lower larval production, lower density dependent predation, thus larger year-classes.

Therefore, density dependent mortality through predation is a control mechanism that serves to produce a tendency toward optimal year-class sizes.

On the ascending portion of the curve, there is no density dependent predation to force the year-class size to an optimal area. Once year-class formation loses its association with density dependent predation, then the recruitment process is almost completely at the mercy of the effect of temperature on larval abundance. A recovery mechanism is the formation of larger 1's with a decline in year-class size, causing earlier

maturation of the year-class if temperature perturbations and competitive interactions form 0-group mackerel are not too interruptive. However, this mechanism is not powerful enough to compensate for extreme drops in year-class size in response to unfavourable temperature since the growth rate of fish will become asymptotic in relation to ration size. A decline in year-class size can never be completely recovered since it leads to a reduction in adult production and subsequent larval abundance. Thus, year-class sizes at the start of a decline are extremely variable, but this variance declines as the production of cohorts becomes less and less. Recoveries can be made when temperature is favourable, but this only prolongs the eventual stock collapse.

The uncertainty in the relationship between stock biomass and larval production (Fig. 10), coupled with the variance in the year-class size larval relationship (Fig. 11) make the scatter in the general Ricker "stock-recruitment" relationship no surprise (Fig. 12). It indicates recruitment is independent of stock size over a fairly wide range. Furthermore, the simulated results indicate the only time any pattern in a stock-recruitment diagram emerged was when the fishery was collapsing. This fact, coupled with the almost impossible task of accurate prediction, makes fisheries management a fairly intangible discipline (Walters 1975).

Implications to fisheries management

To determine the effect of various fishing mortalities on catch (Fig. 13), simulation studies were carried out at two fixed levels of mackerel biomass and year-class size and with mackerel biomass and year-class size oscillating around a biomass of 1.2 x 10^6 m.t. Catch increased gradually in response to fishing mortality for both fixed levels of mackerel biomass and then declined rapidly in response to a recruitment failure of the stock (Fig. 13A, B). However, when the mackerel biomass is allowed to oscillate, catch also increases gradually but does not undergo an abrupt decline (Fig. 13C). The decline in catch is also gradual with the final relationship representing the Schaefer (1954) model.

At a mackerel biomass of 10^6 m.t. the catch of herring

increased more slowly than when biomass was 5×10^5 m.t. A higher yield was also achieved at the lower mackerel biomass level although the upper mackerel biomass level allowed the herring stock to sustain a greater fishing mortality. A recruitment failure occurred at $F_{0.35}$ when the mackerel biomass

was 10^6 m.t., in comparison to a recruitment failure at $F_{0.30}$

when mackerel was at 5 x 10^5 m.t. In both cases, the age group

0 mackerel year-class size was 10⁹ fish. Thus the additional stability in year-class size resulting from a higher level of predation by mackerel is at the cost of a lower yield. The decline in mackerel leads to replacement by herring (Fig. 9). This larger biomass of herring allows for a higher and more easily achieved catch for the same fishing mortality (Fig. 13).

The fluctuations in mackerel biomass seem to give the herring stock an added robustness in addition to higher yield for equivalent levels of fishing mortality. The biological basis of this result is quite complicated, but can be explained in relation to the response of year-class size to predation and larval production. A recruitment failure is usually associated with year-class size and larval production converging on some point on the ascending side of the recruitment curve (Fig. 11). Following this convergence, declines in larval production associated with poor temperature conditions lead to irreversible decline in stock biomass, unless the total mortality experienced by the stock is reduced.

However, when the mackerel biomass is oscillating independently, high biomass levels cause a lower abundance of age group 0 mackerel which accelerates the growth rate of juvenile herring, as well as improving the gonadal production of adult herring. These juvenile herring then reach maturity sooner increasing the size of the overall spawning stock just when the mackerel biomass begins to decline to lower levels. Thus, less predation from mackerel, coupled with favourable temperatures allows for the production of a series of good year-classes which keep the herring stock viable. In addition, the mackerel oscillation prevents the herring larval production from settling into an area on the ascending side of the recruitment curve.

This study would indicate that the determination of maximum sustainable yield (MSY) is better represented by the Shaeffer (1954) type model than the Beverton and Holt (1957) yield per recruit calculation. Winters and Hodder (1975), using a yield per recruit calculation, have determined Fopt (ICNAF Sum. Doc. 1976) for the Gulf of St. Lawrence fishery to be 0.4. This fishing mortality leads to a total collapse in the model developed in this paper. Lett and Doubleday (1976) have already introduced the concept of a critical biomass, the biomass which leads to a recruitment failure; and Doubleday (1976) has discussed the significance of variance in catch in this region. Furthermore, Doubleday (1976) has developed the idea of a "biomass buffer" in reference to an optimal relationship between catch and the variance in catch. In accordance with Doubleday, we have also found that the best representation of fisheries events is by a Schaeffer (1954) type model of catch relative to biomass (Fig. 14), contrary to Beverton's comments of the models simplicity (see Slobodkin 1973). Our model is detailed, including recruitment, environmental perturbation, species interactions, density dependent ℓ_1 growth, and a varying life expectancy for individual cohorts. The maximization of production occurs at exactly 1/2 the virgin stock biomass, yet this is not the area of optimal fishing (Doubleday 1976) since, at this point the uncertainties of catch are indeed great. Following Doubleday's (1976) suggestion we have inspected the area of catch produced by controlling the effort (Fig. 13C) at a level corresponding to an equilibrium biomass of 2/3 the virgin stock biomass. According to the model developed in this paper, it is exactly the area of an optimal tradeoff between variance in catch and catch.

In addition to suggesting viable management alternatives, the simulation of the Gulf of Stl Lawrence herring fishery confirms Ricker's (1954) explanation of the mechanism for the recruitment process. His thesis suggested that density dependent mortality is generated by the aggregation of predators upon the fish larvae and the more larvae the more predation. We feel that this is correct with only one modification and that is, the predators on the larvae is the stock which produced them; therefore, the production of larvae and the number of predators is not independent.

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Appendix I

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Cruise dates utilized for the determination of larval abundance.

1967 May 25 - June 7, Oct 2-8 May 23 - June 3, 1968 -May 12 - May 29, Aug 19-31 1969 May 20 - May 28, Aug 20-29 1970 May 10 - May 20 Aug 24-Sept 3 1971 -1972 May 16 - May 20

Appendix II(A)

Correlation matrix of the intrinsically linear relationship among instantaneous herring growth rate G_a , age group 0 mackerel year-class size M_a, temperature T_m, the dummy variable D, representing spring spawners as 0 and fall spawners as 1, and age group Y_a. (Relates to equation 1). All terms are taken to the log base e.

	G	Ya	T _m	м _у	D	Y _a xT _m	YaxMy	Y _a xD	T_xM m_y	T _m xD	M xD
G	1.00	-0.94	-0.39	-0.66	0.28	-0.93	-0.87	-0.24	-0.62	0.01	-0.09
^Y a		1.00	0.41	0.64	-0.49	0.99	0.92	0.23	0.62	-0.04	0.05
T _m			1.00	0.76	-0.01	0.49	0.60	0.10	0.81	0.03	0.12
м _у				1.00	0.04	0.69	0.81	0.20	0.94	0.06	0.19
D					1.00	-0.05	0.01	0.93	0.01	0.99	0.98
^Y a ^{xT} m						1.00	0.94	0.23	0.07	-0.04	0.05
^Y a ^{xM} y							1.00	0.27	0.79	0.02	0.13
^Y a ^{xD}								1.00	0.15	0.93	0.96
Т _т хМ									1.00	0.02	0.14
Т _т хD										1.00	0.98
MyxD											1.00

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Appendix II(B)

_	^L R	тр	T _p ²	т _р хР	T _p ² xP ²	₽
L _R	1.00	0.15	0.08	0.70	0.43	0.90
T _p		1.00	0.99	0.74	0.90	0.45
Tp ²			1.00	0.71	0.89	0.41
т _р хР				1.00	0.94	0.92
$T_p^2 x^2$					1.00	0.74
Р						1.00

Correlation matrix of the linear model among herring larval production $L_{\rm R}$, production of the adult stock P, and temperature $T_{\rm p}$. (Relates to equation 3).

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Appendix II(C)

Correlation matrix of the intrinsically linear model among herring year-class size Y_p , larval production L_p , and total pelagic biomass 1+ herring and mackerel B_{TP} . (Relates to equation 7). All variables except biomass is transformed to the log to the base e.

	ч _R	LR	L _R ²	В	L _R ² xB
Y _R	1.00	0.64	0.43	-0.10	0.15
L _R		1.00	0.95	-0.50	0.81
L _R ²			1.00	0.46	0.89
^B TP				1.00	0.75
L _R ² xB ₂	[P				1.00



Fig. 1. The spring migration of herring into the Gulf of St. Lawrence is illustrated by the solid arrows, while the fall emigration is shown by the stipled arrow. The dark ring around the Magdalen Islands is an area of spring spawning while the stipled area along the Quebec coast is an area of fall spawning. Historically, some spring spawning also occurred along the Gaspe coast; however, this component has disappeared.



Fig. 2. Effect of 0-group mackerel year-class size and herring age on the instantaneous growth rate of herring. Temperature has been held constant at 14 C.



Fig. 3. Effect of the production of the adult stock on the abundance of herring larvae. Temperature is held constant at 10 C.



Fig. 4. The relationship between year-class of herring at age 2 and their length at end of the first year of life. Fall spawned juveniles have been corrected by the use of a dummy variable to be comparable with spring spawned fish. Arrows indicate the central tendency toward a normal distribution of year-class size and constant ℓ_1 through the maximization of production. Δ 's are fall spawners **O**'s are spring spawners.



Fig. 5. The effect of larval abundance and total pelagic biomass on the formation of year-class size. The back corner of the response has been left out since small herring biomasses will produce few larvae.



Fig. 6. Schematic systems flow chart of the herring recruitment mechanism. Mackerel also interact with herring and are represented by the variables MY, for age group 0 mackerel year-class size and BM for the biomass of 1⁺ mackerel.



Fig. 7. Simulated pattern of herring biomass over time when mackerel biomass is constant at 10^6 m.t. and age group 0 mackerel year-class size is 10^9 fish.



Fig. 8. Simulated pattern of herring biomass over time when mackerel biomass is 10⁶ m.t. and when mackerel are absent from the Gulf of St. Lawrence.



Fig. 9. Simulated tradeoff (open ∆s ± 1S.D.) between herring and mackerel in the Gulf of St. Lawrence. Data points represent real values since 1961; however, there is also the confounding effect of exploitation in the determination of these values.



Fig. 10. A typical simulated relationship between adult herring biomass and larval production.



Fig. 11. A "Ricker type" recruitment relationship fitted to simulated data. The curve represents a diagonal slice through Fig. 5.



Fig. 12. A simulated relationship between herring stock biomass and year-class, showing scatter of points under two extreme situations. Curve is fitted by eye.



Simulated relationship between fishing mortality Fig. 13. Bars represent 1 S.D. of a normal and catch. distribution and different symbols represent different combinations of fishing mortality. Α is when mackerel biomass is 10⁶ m.t. and age group 0 mackerel year-class is 10⁹ fish. ₿ mackerel biomass is 5 x 10^5 m.t. and year-class size of mackerel is the same as A. In C the mackerel biomass is allowed to oscillate in a simulated "virgin state" and mackerel year-class varies in accordance with its biomass and a normally distributed random temperature variable.



Fig. 14. Simulated relationship between total herring stock biomass and catch. Bars represent 1 S.D. Mackerel biomass has been allowed to oscillate in a simulated virgin state.