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The influence of temperature on the interaction of the recruitment mechanisms of Atlantic herring and mackerel in the Gulf of St. Lawrence

by

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Introduction

The Atlantic mackerel (*Scomber scombrus*) are schooling fish which reach a maximum length of 55 cm and generally mature at 2 years of age, at a length near 35 cm. They overwinter in the Gulf of Maine at depths between 100-200 m along the outer part of the Continental Shelf (Sette and Needler 1934, Sette 1943). During the spring, the stock component used in this analysis, migrates north to the Gulf of St. Lawrence to spawn where they remain resident until October. At this time they interact with an Atlantic herring (*Clupea harengus*) population made up of a spring and fall spawning component (Day 1957).

Annual changes in water temperature are known to cause fluctuations in the abundance of both species (Taylor et al. 1957, Posthuma 1971). In an attempt to link up the environmental effects with those due to changes in parent stock biomass, egg and larval surveys were initiated in the southern Gulf of St. Lawrence. However, only pelagic mackerel eggs could be used in the analysis since herring eggs remain benthic.

It is the aim of this paper to analyse the effect of the interaction of temperature, and to a less extent salinity, as key environmental factors, with parent stock biomass in determining the stock recruitment mechanism for both species. It is also anticipated that some insight will be gained into the interaction of the recruitment mechanisms of the two species.

Methods

In 1965 an investigation of the distribution and abundance of fish eggs and larvae in the southern Gulf of St. Lawrence was initiated and subsequently continued until 1974. For the present analysis only the samples from three types of nets were considered, standard conical meter nets, Miller samplers, and 24" bongos (Kohler et al. MS 1974).

Volumes of water strained by the standard conical meter nets were measured with TSK flow-meters (Tsurumi-Seiki Kosakusho Co. Ltd., Yokohama, Japan). The nets, stacked on a wire at various depths, were towed simultaneously at 2 1/2 knots, each for half an hour. The conical meter nets and bongos were towed at 0 and 15 m, the Miller samplers were towed at 5 m intervals up to 40 m. Not all depths were covered at any one time. The ships used for these cruises were the *M.V. Harengus* and *C.G.S. E.E. Prince* and *A.T. Cameron*.

The nets were thoroughly washed down with salt water when brought aboard after towing. Samples were routinely stored in 32-oz glass bottles. Special effort was made in the identification of eggs and larvae between 1965 and 1974. Larvae were separated by their irregularities in pigmentation (Bigelow and Schroeder 1953). When there was any doubt concerning the species to which the eggs belonged, they were incubated and the hatched larvae subsequently identified.

Preliminary data analysis

Some amalgamation of the large amounts of data collected between 1965 and 1974 was necessary before any analysis was possible. The strong auto-correlation between successive tows within a cruise indicated the best method to observe unbiased patterns within the data was to treat an entire cruise as one experimental unit. The analysis of the data could then be treated as a multiple split plot design (Cochran and Cox 1968) with cruises being the main plot. The first split within cruises was a breakdown of gear types, all adjusted to a constant amount of water strained (100,000 cu m); thus catches of the largest gear type were reduced and the catches of the smaller samplers were increased. Those with a different mesh size in the codend (#471 Nitex) were not used in the analysis. Calculated flows on the meter nets did not differ from the observed flows taken by the TSK flow-meter by more than 5%. This level of accuracy was assumed to apply to the calculated flows for the other nets. The next split, within gear, was depth.

Preliminary analysis of the gear types showed that adjusted egg and larvae catches for Miller samplers, one-meter nets, and bongo nets were not significantly different. Catches in the other types of gear were an order of magnitude lower than these, and were not comparable. Depth was not found to be significant in determining egg and larvae availability, therefore, tows at different depths were used as an estimate of pure error (Draper and Smith 1966). The mean sea surface temperatures were calculated for each depth and gear type while a mean salinity was used for an entire cruise.

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

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

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

Results

Mackerel

Analysis of the catch of mackerel eggs/100,000 cu m of water strained indicated that modal egg abundance occurred usually in June, when the sea surface temperature was at 10°C. In accord, Sette (1943) found that 98% of the egg catch was in water between 9.0°C and 13.5°C, and that this may be regarded as the range in which the bulk of mackerel eggs are usually spawned in the region. A distinct dome-shaped, quadratic relationship exists between estimated parent stock biomass (B) and the log of the modal catch of eggs/100,000 cu m of water strained (Eg) (Fig. 1). Virtual population analysis (Pope 1972) was used by Anderson (MS 1975) to determine the numbers of fish in each year-class, these numbers being multiplied by the mean weight for each age to determine biomass. The equation describing the relationship is as follows:

$$(1) \log_{10}(Eg+1) = 1.63 \times 10^{-2} B - 1.25 \times 10^{-5} B^2$$

The coefficient of multiple determination (R^2) was 0.909 while F for regression was 30.31*.

Egg abundance levels predicted by equation (1) agree with Sette's (1943) observation that a mackerel stock can potentially spawn widely varying densities of eggs, so that a doubling of stock size can result in a change in egg abundance of three orders of magnitude. This variation undoubtedly is in part due to mackerel having the ability to stagger spawning, producing only 40,000-50,000 eggs at one time, although females of medium size can broadcast from 360,000-450,000 eggs (Bigelow and Welch 1925). However, egg mortality for mackerel has been calculated at as low (20%) (Sette 1943) due to the short incubation time (\approx 7 days). Also since the majority of eggs are spawned at approximately 10°C, temperature differences would presumably account for little mortality.

Low egg mortality would mean that there is a potential for large numbers of larvae (Fig. 2). However, the relationship between the numbers of eggs and the resultant larvae is strongly density dependent since the growth rate of mackerel larvae is extremely high, (12.5%/day in weight (Royce 1972)) and the larvae are cannibalistic (Arnold 1970).

An intrinsically linear model (appendix 1) was fitted to the relationship among catch of eggs/100,000 cu m of water strained (Eg), time in days since the sea surface temperature was 10°C in the Gulf; and the catch of larvae (L_R)/100,000 cu m of water strained.

The accepted equation based upon the minimum error mean square is:

$$(2) \log(L_R+1) = -1.2371 \log(Eg+1) \times \log Tm + 2.2567 \log(Eg+1)$$

Variable	Standard Error	Partial Corr. Coeff.
$\log(Eg+1) \times \log Tm$	0.2354	-0.8456
$\log(Eg+1)$	0.3896	0.8677

The coefficient of multiple determination is 0.809, while the overall F for regression was 23.41*.

*Significant at $P \leq 0.05$

The initial number of eggs varies considerably, although the resultant numbers of larvae are similar, after 30-40 days. These results correspond with the finds of Harding and Talbot (1973) for plaice (*Pleuronectes platessa* L.). On day 40 an initial catch of 1,000 eggs results in a catch of 8 larvae, in contrast to 100,000 eggs leaving only 32 larvae. Furthermore, equation (2) can be used to show that on day 12 the number of larvae almost equals the catch of eggs, confirming Sette's (1943) observation that egg mortality in mackerel is low. As previously noted, the incubation time of mackerel eggs is about 7 days, and the yolk sac is completely absorbed within 5 days (Sette 1943) for a total of 12 days. Therefore, the major mortality of mackerel larvae commences with active feeding.

Thirty days was chosen as approximately the midpoint through the larval stage (Sette 1943). A relationship was found between the numbers of larvae on day 30 and the estimated year-class size at age 1+ (Fig. 3), from virtual population analysis (Anderson MS 1975).

The intrinsically linear model fitted to the relationship is:

$$(3) Y_R = 117.3 + 71.569 \times T_p \times [\text{Log}(L_R + 1)]^2$$

The coefficient of multiple determination (R^2) is 0.901 while F for regression is 62.89*. The addition of $b \cdot \log(L_R + 1)$ to provide a density independent and dependent mortality term only explained an additional 2.0% of the total sums of squares. Thus the $T_p \times [\log(L_R + 1)]^2$ interaction was used to describe the relationship between year-class size and larval abundance, the quadratic nature of the logarithm of larval abundance causing the relationship to approach an asymptotic value more quickly. Only the linear effect of temperature was tested but was significant. The annual maximum mean monthly sea surface temperatures at Grande-Riviere were used throughout the analysis. (Lauzier MS 1969).

Equation 1-3 were singularly significant and not fitted to errors, (since F values were all greater than 4 times the required F'), in describing discrete portions of the egg, larval, and juvenile biology of mackerel. However, a simplification was constructed to test the predictability and behavior of the equations as a system. A family of stock, recruitment curves were simulated (Fig. 4) which were consistent with the imperial observations. W. G. Doubleday (personnel communication) suggested that a functional relationship between recruits/unit temperature and estimated mackerel recruits/unit temperature and estimated mackerel biomass should be conserved within the system. The results of this manipulation displayed a stock recruitment curve (Fig. 5) with little associated variance somewhat different than any proposed by Ricker (1954), Beverton and Holt (1957) and Cushing and Harris (1973). The maximum of this imperically fit relationship occurred at a mackerel biomass of 650×10^6 kg; the biomass which also produced the maximum in the statistically fit egg production curve (Fig. 1) and the simulated stock-recruitment relationship (Fig. 4).

Herring

The catch of spring spawning herring larvae varied in response to both the maximum mean monthly sea surface temperature at Grande-Riviere, and spawning stock biomass (Fig. 6). The effects of salinity on larval catch were also tested however, in accord with Alderdice and Velsen (1971) the large standard error associated with the main effect and temperature interaction indicated it was of little predictive

value. The whole linear model and correlation matrix can be found in appendix II.

The accepted equation, based on the minimization of the error mean square, was fitted by stepwise regression:

$$(4) L_{RS} = 38.553B - 0.412B^3 + 304.439Tp - 10.237Tp^2 - 1.428 BxTp - 2270.179$$

Variable	Standard Error	Partial Corr. Coeff.
B	16.779	0.443
B ³	0.128	-0.567
Tp	106.596	0.520
Tp ²	3.568	-0.522
BxTp	0.989	-0.294

The coefficient of multiple determination was 0.636 while F for regression was 7.713*. B is 10⁻⁶ times the total estimated biomass in kg. The parent stock biomass estimated from virtual population analysis (Winters and Hodder MS 1973) were for herring 4+ and older. The numbers of fish in each age group were multiplied by the mean weight of that age group. Tp is the maximum mean monthly sea temperature at Grande-Riviere for each year, and L_{RS} is the catch of spring spawned larvae/ 100,000 cu m of water strained.

Since there was no significant trend in the catch of larvae over depth, multiple tows at different depths were used as an estimate of pure error (Draper and Smith 1966), although they showed considerable variation (20% of total variation). Furthermore, the effect of variation in survey intensity produced a considerable problem, which was overcome by giving more weight to years with more intense surveys. The addition of time as the independent variable produced spurious results presumably due to the prolonged spawning period of herring. In the analysis, more weight is given to those years with more intensive surveys.

The catch of fall spawning herring larvae showed a similar response, to temperature and estimated parent stock biomass as spring spawned larvae. However, since the fall spawning stock was historically about twice the size of the spring spawning stock and was fished less intensively (Winters and Holder MS 1973) a response over the entire range of fall biomasses is not available (Fig. 7). Salinity was not included as a variable in the analysis of fall spawning larvae, since it varied over a narrow range and was not significant in explaining the variations in abundance of the spring spawned larvae.

The whole linear model and correlation matrix are in appendix III for the following accepted equation:

$$(5) L_{RF} = -133.652B - 0.051B^3 - 3.274Tp^2 + 8.973BxTp + 795.470$$

Variance	Standard Error	Partial Corr. Coeff.
B	28.969	-0.853
B ³	0.041	-0.399
Tp ²	0.637	-0.876
BxTp	2.055	0.839

The coefficient of multiple determination (R²) is 0.936 while F for regression is 29.18*. L_{RF} is the catch fall spawned larvae/100,000 cu m of water strained. The cubic

nature of biomass indicates that catch of eggs per unit change in biomass increases at a rate somewhat less than the rate at which it subsequently declines (Fig. 6). The effect of temperature for both stocks is negatively quadratic and therefore reaches some optimum value. This observation agrees well with those made by Blaxter (1956) for the survival of herring eggs. The B x Tp interaction was also significant in determining the numbers of larvae from both stocks, however this interaction causes the biomass optimum (Fig. 6-7) to decline with temperature for spring spawned larvae but has the opposite effect in influencing the survival of fall spawned larvae.

The total pelagic biomass, made up of both mackerel and herring is having a profound effect on the abundance of 2⁺ herring recruits (G. H. Winters, personal communication). Furthermore, the number of surviving larvae is also an extremely important variable (Fig. 8). The intrinsically linear model fitted to the data was:

$$(6) Y_R = 2910.620 \log_{10}(L_R+1) - 0.798 \times B_T \times [\log_{10}(L_R+1)]^2 + 163.920$$

Variable	Standard Error	Partial Reg. Coeff.
$B_T \times [\log_{10}(L_R+1)]^2$	0.099	-0.858
$\log_{10}(L_R+1)$	317.475	0.889

The coefficient of multiple determination was 0.820 while F for regression is 43.59*. Y_R is the estimated year-class size from virtual population analysis (Winters and Hodder MS 1973), L_R is the total catch of spring and fall spawned herring larvae /100,000 cu m water strained and B_T is the estimated total pelagic biomass. The relationship indicates there are varying degrees of density dependence, responding to different levels of total pelagic biomass. The $\log_{10} L_R \times B_T$ interaction is the dominant variable determining year-class size of herring. Temperature, as it effects larval abundance, is only important when the pelagic biomass is high. At intermediate levels of pelagic biomass (300-1,200 x 10⁶kg) temperature has little effect on year-class success.

Discussion

Mackerel

The density-dependent response of the catch of mackerel eggs to estimated parent stock biomass is indeed profound (Fig. 1). However, a similar response was reported for the catch of cod eggs in the Gulf of St. Lawrence (Lett et al. MS 1975). Bagenal (1966) noted that fecundity of plaice, of equal size, rose with an increase in fishing mortality. Both Scott (1962) and Tyler and Dunn (1975) found that the fecundity of rainbow trout and winter flounder respectively, responded to different feeding levels. Bagenal (1966) related the changes in fecundity of plaice to an increase in the availability of food due to a reduction in population biomass. He went on to conclude that if the fecundity of the population is modified by food availability, the fecundity acts as a density-dependent population regulating mechanism, in the manner noted for cod and mackerel.

The logarithmic nature of egg abundance is presumably related to the ability of mackerel to spawn in nine discrete intervals (Bigelow and Welch 1925). If the frequency of ova maturation and fecundity are related to food supply, the observed variations in egg abundance are indeed conceivable. Since mackerel school, filter feeding on plankton, it is

possible for them to overcrop their food resource within a limited area. If the rate of food intake of a large biomass of mackerel was greater than the rate of plankton production, the standing crop of plankton could be severely reduced. It is doubtful that the food resource would be totally cropped, since fish adjust their feeding rate in response to food density (Ware 1975) and plankton are aggregated rather than uniformly distributed. However, this mechanism could lead to a dramatic reduction in available food within a short period. The works of Brooks and Dodson (1965), Galbraith (1967), and Brett (1971) have shown that pelagic fish can have a dramatic effect on both the size composition and abundance of available zooplankton.

The survival of mackerel larvae is determined by a "productivity gate," similar to that suggested by Hempel (1965), which only allows a limited range in the numbers of surviving individuals to pass through (Fig. 2). This hypothesis implies a regulatory mortality which compensates for differences in the number of eggs. The magnitude of the responses of egg abundance and larval mortality to density dependence seems to have made environmental effects insignificant.

The diet of mackerel larvae in the Gulf of St. Lawrence is primarily copepods, although a substantial portion has been found to be other mackerel larvae, when they have grown to a length of 11-50 mm (Arnold 1970). This coupled with their unusually high growth rate is perhaps the basis of the density dependent mechanism. Similar responses have been demonstrated for sardine and anchovy larvae (Issacs 1965), and plaice larvae (Harding and Talbot 1973). However, cod (Lett et al. 1975) and herring larvae (present study) seem to show little density dependence. Probably, starvation and subsequent predation are the two main causes of larval mortality in all these stocks, with cannibalism being of less importance.

The year-class strength of mackerel is also determined by a density-dependent relationship which interacts with temperature (Fig. 3). Since the relationship tends to reach an asymptote, and not decline, it is probably more related to the carrying capacity of the system than the attraction of predators; which seems to be more the case for demersal systems (Lett et al. MS 1975). The carrying capacity increases with a rise in temperature.

The amalgamation of the relationships determining egg, larvae, and adult abundance is demonstrated in figure 4. Maximum recruitment occurs at an estimated stock biomass of 650×10^6 kg with recruitment declining symmetrically at both larger and smaller biomasses. This observation agrees well with the plotted imperial data (Fig. 5) which also involves the interaction of temperature. The effect of temperature is to improve recruitment when biomass is at the optimum level. This results from the numbers of larvae increasing with stock biomass leading to a more profound effect of the interaction with temperature until the optimum biomass is reached. Further increases in biomass cause a reduction in the numbers of larvae thus diminishing the effect of temperature.

Herring

The survival of herring eggs until the larval stage might be fitted by an optimum (Posthuma 1971), similar to that noted for spring spawned larval abundance in the Gulf of St. Lawrence (Fig. 6). An increase in spawning stock biomass

from 1×10^5 to 6×10^5 metric tons caused the temperature for optimum larval abundance to decline very little (14.80 to 14.45°C). This shift in optimum temperature may be related to a change in egg size accompanying a decline in stock biomass (Bridger 1960, 1961), since egg size is influenced by feeding conditions prior to spawning (Hempel 1971). Stock biomass also has an optimum level for maximum larval survival. The argument supporting this relationship is similar to that for mackerel.

The decline in larval numbers with increasing biomass may be due to extrinsic density dependence. The accumulation of egg layers on the bottom could lead to local oxygen minimums or the concentration of predators (Galkina 1971). However, Parrish et al. (1959) and Runnstrøm (1941) state that only rarely would egg sheets be detrimentally thick for Atlantic herring, since they spawn on shoals rather than inshore on shallow beaches (Alderdice and Velsen 1971).

There is some evidence of intrinsic density dependence for spring spawning Gulf of St. Lawrence herring fecundity. A 58% increase in the fecundity of 340 mm herring was noted with a 55% decline in biomass between 1967 and 1970 (Barrett MS 1967; Messieh unpublished data). Furthermore, the percentage increase in fecundity depended on the length, larger fish showing greater fluctuations than smaller ones.

The decline in larvae at estimated stock biomasses greater than 3.5×10^5 metric tons was cubic, rather than quadratic, as noted for mackerel and cod (Lett et al. MS 1975). This may be linked to the additive effects of density dependence of eggs abundance and larvae, although Hempel (1965) suggests density dependence in herring larvae is relatively weak.

The relationship among larval abundance, temperature and estimated parent stock biomass was similar for fall spawning herring (Fig. 7). Larval abundance declined over the range of annual temperatures seen in the Gulf of St. Lawrence, presumably due fall spawned larvae being better adapted to survive in cooler waters.

There is little difference in the size of spring and fall spawned juvenile herring at years of age. For this reason, the catches of spring and fall larvae were combined to be compared with the numbers of 2⁺ fish. The degree of density-dependence is governed by the interaction of total pelagic biomass (Fig. 8). At low pelagic biomass, herring recruitment is similar to the relationship previously noted for mackerel larvae with the productivity of the system limiting the survival. However, as the pelagic biomass increases, the curved right-hand limb begins to drop and become concave, suggesting predatory activity. It is not unreasonable to postulate that when pelagic biomass is raising and the carrying capacity remains constant adult herring and mackerel may prey on herring larvae, as an alternate food resource. The high pelagic biomasses were made up of 80% mackerel biomass suggesting mackerel may be more predatory than herring. An alternate hypothesis is that adult mackerel and herring outcompete the 1⁺ and 2⁺ juveniles for available food, making them more susceptible to predation through starvation, thus elevating their mortality rate.

Interestingly, the mackerel biomass which gives the most stable recruitment is one which also produces stable herring recruitment, when mackerel and herring biomasses are of approximately equal size. It would seem these two species are playing an evolutionary game with the optimal strategy for success being community stability, fitting within the productive constraints of their environment.

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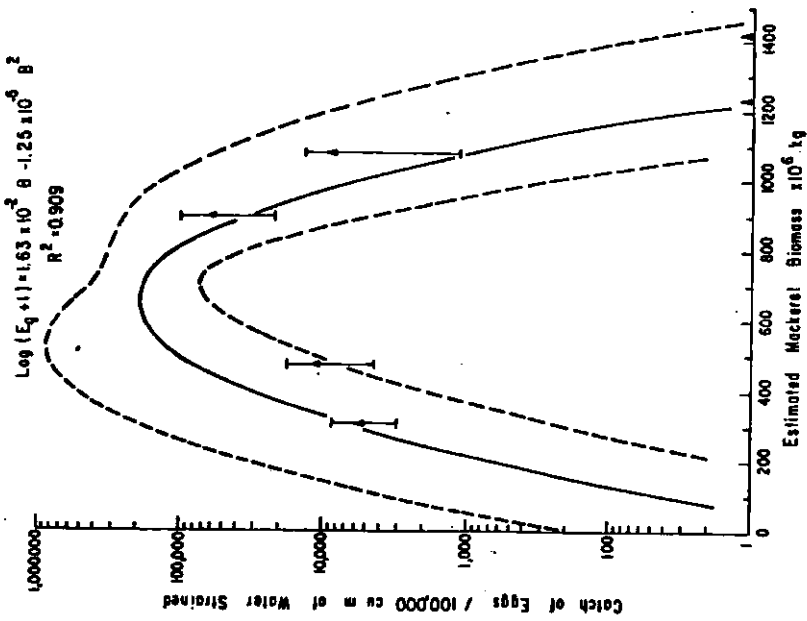


Fig. 1

Density-dependent relationship between estimated mackerel parent stock biomass and the logarithm of the catch of mackerel eggs/100,000 cu m of water strained.

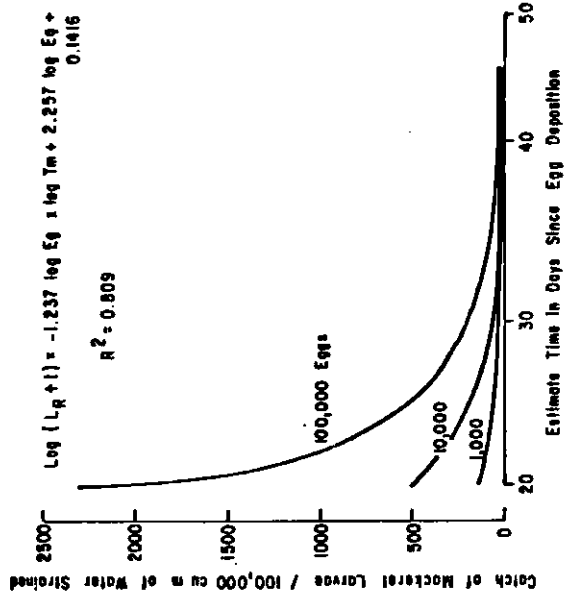


Fig. 2

Density-dependent mechanism for mackerel larvae generated through time.

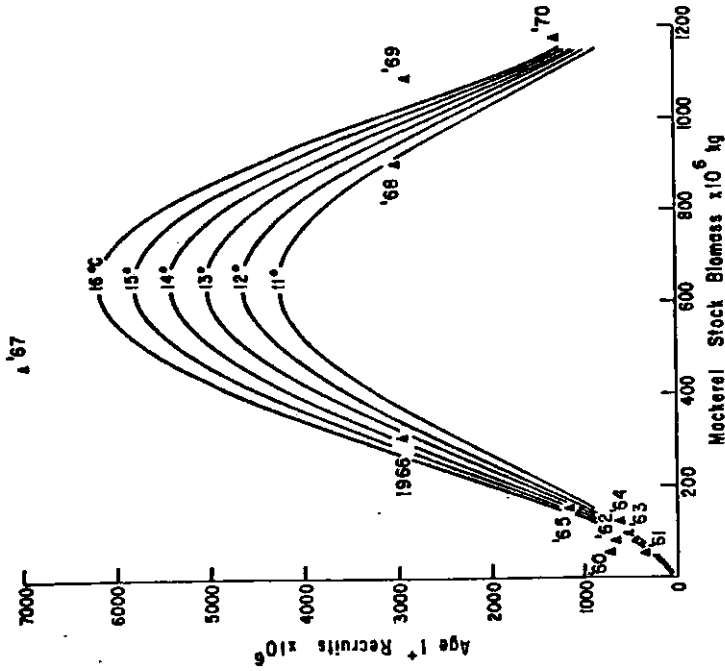


Fig. 3

Density-dependent relationship between the catch of larvae/100,000 cu m of water strained and the estimated number of 1+ mackerel from virtual population analysis. The interaction with temperature rises as the number of larvae increases.

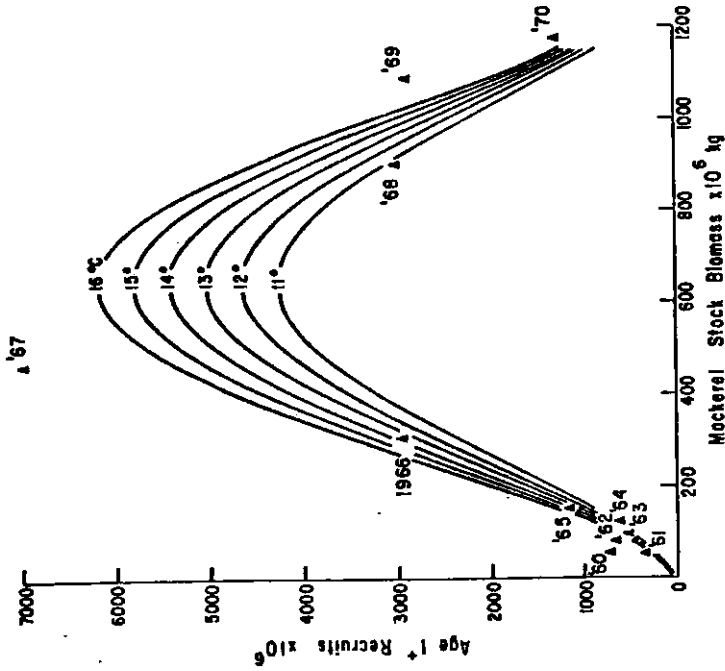


Fig. 4

The simulated stock, recruitment curve for different temperature maximums. The points on the graph are imperial data.

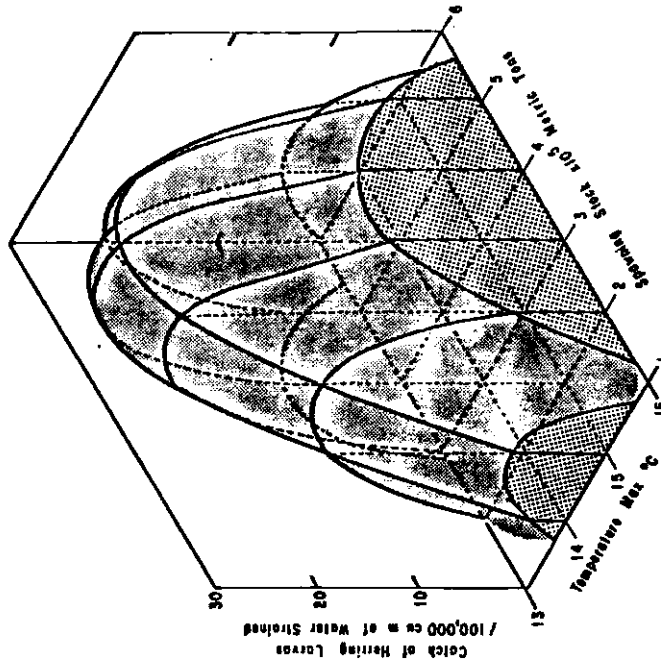


Fig. 6

Catch of spring herring larvae/ 100,000 cu m of water strained in relation to spawning stock biomass and temperature.

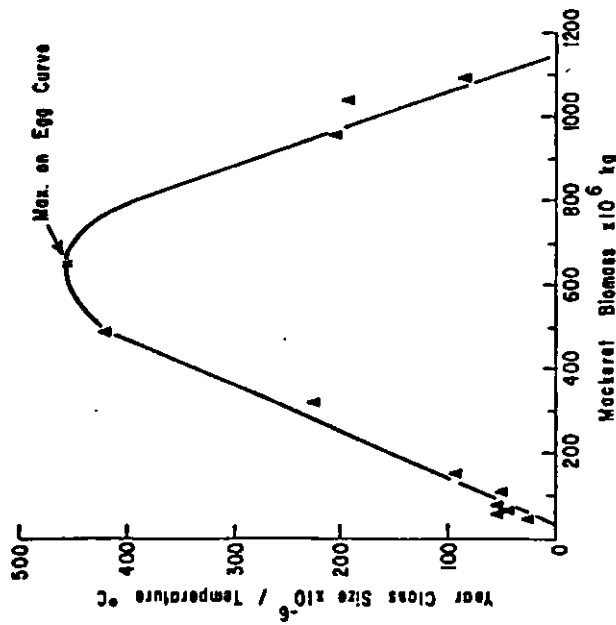


Fig. 5

The empirical fit of year-class size/unit °C in relation to biomass. The maximum of this curve corresponds with the maximum of the egg production curve.

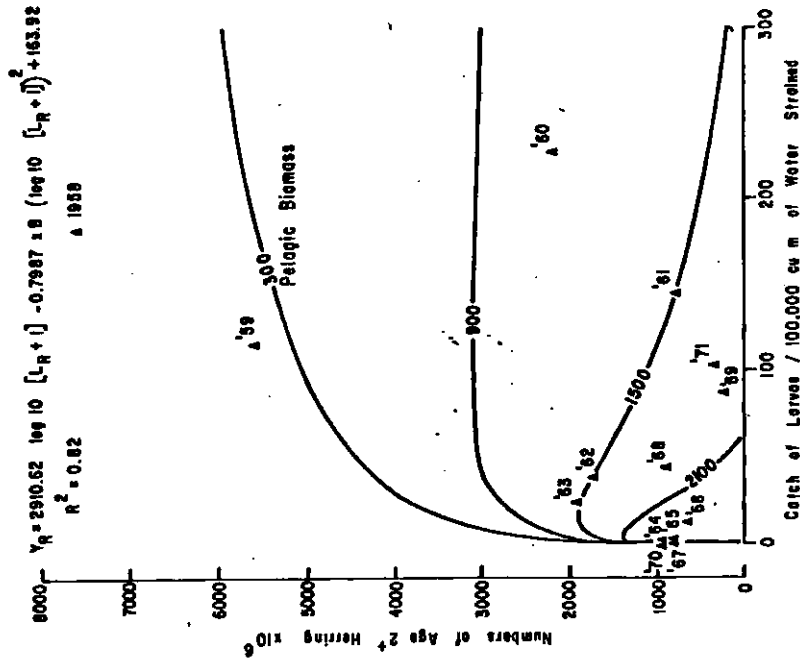


Fig. 8

Density-dependent relationship between herring larvae and estimated year-class size from virtual population analysis. The total pelagic biomass (mackerel and herring) influences the degree of density of density dependence.

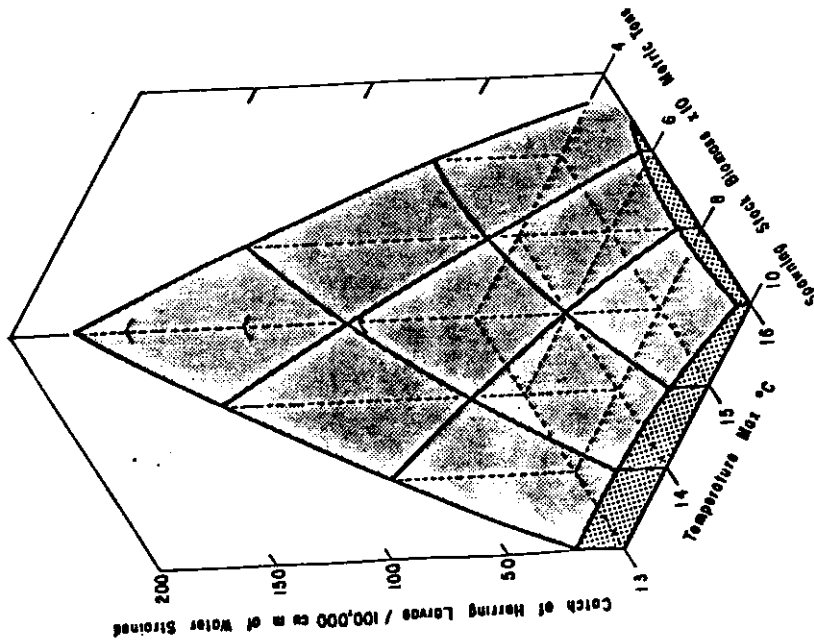


Fig. 7

Catch of fall herring larvae/100,000 cu m of water strained in relation to spawning stock biomass and temperature.

Table 1. Correlation matrix of the whole model of equation(2)

	$\log(L_R+1)$	$\log(Eg+1)$	$[\log(Eg+1)]^2$	$\log(Eg+1) \times \log Tm$	$[\log(Eg+1)]^2 \times \log Tm$
$\log(L_R+1)$	1.000	0.577	0.543	0.041	0.479
$\log(Eg+1)$		1.000	0.990	0.216	0.991
$[\log(Eg+1)]^2$			1.000	0.217	0.987
$\log(Eg+1) \times \log Tm$				1.000	0.243
$[\log(Eg+1)]^2 \times \log Tm$					1.000

Table 2. Correlation matrix of the whole model of equation(4)

	L_{RS}	B	B^2	B^3	Tp	Tp^2	Sal	BxTp	BxSal
L_{RS}	1.000	0.117	0.018	-0.044	-0.478	-0.481	0.021	0.035	0.122
B		1.000	0.979	0.940	0.306	0.052	-0.203	0.978	0.997
B^2			1.000	0.989	0.033	0.054	-0.201	0.950	0.978
B^3				1.000	0.006	0.027	-0.167	0.901	0.943
Tp					1.000	0.999	-0.316	0.219	0.008
Tp^2						1.000	-0.323	0.239	0.028
Sal							1.000	-0.291	-0.154
BxTp								1.000	0.971
BxSal									1.000

Table 3. Correlation matrix of the whole model of equation(5)

	L_{RF}	B	B^2	B^3	Tp	Tp^2	BxTp
L_{RF}	1.000	-0.822	-0.822	-0.820	-0.348	-0.367	-0.848
B		1.000	0.994	0.979	0.253	0.474	0.985
B^2			1.000	0.996	0.041	0.062	0.983
B^3				1.000	0.062	0.082	0.973
Tp					1.000	0.999	0.192
Tp^2						1.000	0.213
BxTp							1.000