The natural mortality of the plaice

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During their life histories fish grow up through the trophic levels of the marine ecosystem and it can be argued that their mortality due to predation is a density-dependent function of age. Such a function is derived formally and is applied to the plaice; a curve of mortality was calculated from larval life to the critical age of sixteen years, at which the specific growth rates and mortality rates become equal. For older fish an attempt was made to show that a senescent mortality takes place, i.e. after the critical age. In a study of stock and recruitment, if the trend of natural mortality with age can be established, then cohorts can be considered to have replaced themselves on average by the critical age. Therefore replacement is contained within the system as it must be and there is no need to establish a replacement stock, as for example in the Ricker curve.

Introduction

When the dependence of recruitment on parent stock is studied in multi-aged spawning stocks, it is desirable to establish the trend of natural mortality with age. Natural mortality is often assumed to be constant, and in most stock assessments the assumption is reasonable. Thus a cohort in the virgin stock must live for a very long time and the magnitude of the virgin stock is theoretically inaccessible. The concept of replacement stock (in Ricker's 1954 sense) is then imprecise in the multi-aged spawning stock, yet it is an essential part in Ricker's equation relating recruitment to parent stock. The great majority of Pacific salmon die after their only spawning, and an estimate of natural mortality is not needed to establish the replacement stock. The method cannot theoretically be extended to fish that spawn repeatedly, until the trend of natural mortality with age can be established.

From a series of life tables, Deevey (1947) examined the trend of natural mortality with age for a variety of animals. Common to all is a downward trend in mortality during the juvenile stages to sexual maturity. Equally, there is in most an upward trend in mortality amongst the older animals. During the first stage, in immature life, mortality declines as numbers decrease, but in old age it increases with falling numbers. The latter, which may be senescent mortality, is possibly a property of individuals, whereas that of the immature age groups may be a property of the population. For the plaice of the southern North Sea, this paper attempts to describe, first, natural mortality as a density-dependent function of age during juvenile and adult life and, secondly, the possible course of senescent mortality.

Density-dependent mortality

Most marine fishes are very fecund and lay between 10^4 and 10^7 eggs. The decline in numbers during immature life is very marked indeed. Pearcy (1962) has shown that mortality declines in time during the larval life and immature life of the winter flounder (*Pseudopleuronectes americanus* Walbaum) and that it decreases more slowly with increasing age. Mortality declines as density decreases with age, and there may be a density-dependent mortality which is a function of age.

It is generally recognized that the control of numbers in fish populations is achieved by density-dependent processes in juvenile life rather than by variations in fecundity (in adult life). Harris (1975) has distinguished stock-dependent processes from density-dependent ones. The initial number of eggs is generated by the stock which exercises control from generation to generation; stock dependence in Ricker's equations is obtained by the aggregation of

predators of the initial numbers of eggs or larvae. Beverton and Holt (1957) developed an equation identical in form in which control is also stock-dependent. If the larvae grow quickly through a critical period of predation (the duration of which is proportional to stock), the mortality is low and vice-versa. It is proposed here to extend the critical period indefinitely, because fish continue to grow throughout their lives and are always subject to predation. However, the critical period of Beverton and Holt is stock-dependent and any extension, to the age of recruitment, could not be so. The extended period is one in which mortality is density-dependent. The essential problem in studies of stock and recruitment is to find a formulation which is stock-dependent and density-dependent, which is based on the availability of food and which can generate a dome-shaped curve.

If the predominant source of mortality is predation, then it is likely to be density-dependent. Predatory processes may be simplified as follows. The time taken in predation may be divided into the time to handle and eat and the time to search. The first is independent of density and the second is inversely proportional to it. Because the searching time is usually greater than the handling time amongst plankton animals, predation is a density-dependent function. All mortality in fishes may ultimately be due to predation in the sense that a sick fish dies by being eaten. Then it would be reasonable to suppose that the natural mortality of fish was effectively density-dependent. As fish grow, they pass through a succession of predatory fields, in each of which the chance of death is less than in the previous one, merely because both fish and predator are bigger. Growth is a function of age, and natural mortality may well be a density-dependent function of age.

In a stock and recruitment curve there is more variability in recruitment than in stock; that in recruitment is environmentally determined. The enormous loss of numbers during immature life is sometimes considered as a response, in evolutionary terms, to a hostile environment; in other words, most of the loss by density-independent mortality is waste. However, analysis of the Ricker equation (Ricker, 1973) shows that the proportion of density–independent mortality exceeds that of density-dependent mortality. If the latter were a continous process then density-independent losses would be modulated subsequently in a density-dependent manner and the two processes would be hard to separate. Jones (1973) and Cushing and Harris (1973) have suggested that larval mortality of a cohort may express the best extraction of food available during the pre-recruit life

of a cohort, a response to a benign environment. Gulland (1965) proposed that there was a coarse and a fine control of recruitment; stock-dependent mortality would provide the coarse control and density-dependent mortality throughout immature life would provide the fine control.

A female fish may spawn for n years and to replace itself it must generate two spawning adults by the end of its life, or $2/n$ per year. Ricker (1945) has defined a critical length in a population as that at which the growth rates and mortality rates are equal. There should equally be a critical age (T) at which the specific growth rate, G, equals the specific mortality rate. Thus $G = (1/t) \ln (W_2/W_1)$, where W_1 is weight in a given year and W_2 that one year later; then the specific mortality rate $M^* = (1/t)\ln (N_1/N_2)$, where N_1 is the number in a cohort in a given year and N_2 that in the same cohort one year later. The cohort adds biomass to the stock to replace losses; within the life of the cohort biomass reaches a maximum at the critical age in the unexploited stock and after tha age no increment in stock can be expected. Hence the cohort should have replaced itself in numbers. The idea of a cohort replacing itself is a difficult one. The initial number in a cohort is a function of stock and the stock replaces itself each year as the cohort reaches the critical age. The pattern of growth and mortality is determined between hatching and recruitment and so the mode of replacement of stock each year is independent from cohort to cohort. Fish of ages greater than the critical age will of course contribute to the fecundity of the population. The virgin stock varies in magnitude: if it has more than replaced itself in the numbers of eggs produced, the density-dependent processes in the subsequent generation will reduce the excess, and if it has failed to replace itself by the critical age then the fecundity of the older fish should make up the deficit. If fish became senescent in old age, the process might be expected to start after the critical age. Greer-Walker (1970) has shown that the white muscle fibres of large cod decrease in size as they grow older, so the attack and escape speeds must decline. The senility function might reduce the biomass of older fish in age in such a way that the ratio of older stock to total stock corresponded to the coefficient of variation of the recruitment to the virgin stock. If senescence is a physiological property of the individual, the population processes will not be changed with the quantity of stock, i.e. the trend of senescence with age after the critical age will always be the same.

Let us suppose that natural mortality is a density-dependent function of age between hatching and the critical age.

Let $N_t = N_{(t - \delta t)}e^{-kN_t \cdot \delta t} \simeq N_{(t-\delta t)}(1 - kN_t \cdot \delta t + \ldots \ldots)$

As $\delta t \to 0$, $N_{(t - \delta t)} \to N_t$

$\therefore N_t - N_{(t-\delta t)} = \delta N_t \simeq -kN^2_t \, \delta t$, for small δt

$$\int \frac{dN_t}{N_t^2} = -\int k \, dt$$

$$\therefore \left[-\frac{1}{N} \right]^{N_t}_{N_0} = \left[-kt \right]^t_0$$

$$\therefore -\frac{1}{N_t} + \frac{1}{N_0} = -kt \therefore N_t = N_0/(1 + N_0 kt)$$

Let $kN = M$; $N_t = N_0/(1 + M_0 t)$; $M_0 = (N_0 - Nt)/(N_t \cdot t)$.

This derivation is due to my colleague, Mr J.G.K. Harris.

The formulae may be applied as follows. Let N_0 be the initial number, i.e. at hatching or at first feeding, and let T be the critical age. Then $M_0 = (N_0 - N_T)/N_T \cdot T$; in the virgin stock of plaice $N_T = 2$ and $T = 16$. An estimate of M_0 can be made if the ratio (N_t/N_0) is known, for example, in the initial mortality rate of plaice larvae. Then N_0 can be estimated.

Larval mortalities, in so far as they are known, are high and trial calculations show that M^* is the same at any age greater than three years old if N_0 is large. In such terms, cod, herring and sprat may have the same mortality rates at a given age, but throughout adult life their average mortality rates differ considerably because their ages of first maturity and their critical ages differ considerably. As it becomes possible to estimate larval mortality and initial numbers more accurately, specific differences in natural mortality may well emerge. The natural mortality rate of tuna is 0·7 (Schaefer, 1957; Suda, 1970), but as compared with other fishes it is anomalously high and there may be a component of emigration in the estimate.

In adult fishes density-dependent growth has rarely been detected. In juvenile fishes it is relatively well established in gadoids (Raitt, 1939) and in herring (Iles, 1967). In the Pacific halibut, density-dependent growth persists into the early adult age groups, but in older fish it dies away. Provisionally it may be assumed that there is no density-dependent growth in the mature age groups. Then the critical age is easily determined.

The natural mortality of the plaice of the southern North Sea

Hempel (1955) showed that density-dependent growth could not be detected in the adult age groups of plaice in the German Bight of the southern North Sea. I have examined the data from the Lowestoft catches between 1929 and 1970 and could also find no density dependence by plotting the ratio of weight increment to weight on stock density at the age of five. However, the mean length of five year-old fish increased by about 5 cm during the fifties, which is a considerable increment, and Gulland (1968) has suggested that there was a shift of fishing effort from the Southern Bight to the eastern North Sea, that is, on to the larger fish in an age group. However, comparing Hempel's data with those from Lowestoft, the German Bight fish tended to be a little smaller than those of the Southern Bight up till 1955. To obtain an estimate of growth, the year-classes 1942, 1943 and 1944 were chosen, partly because the increase in length was least in these year-classes and partly because they were represented in the data used in the later study of senescence. For females only, the parameters of the von Bertalannfy growth equation, $L\infty$, the length at infinite age, k, the rate at which $L\infty$ is approached, and t_0, the age at which growth starts (in a statistical sense), were as follows:

Year-class	k	$L\infty$ (cm)	t_0 (years)
1942	0·1140	61·00	
1943	0·0748	71·67	
1944	0·1054	61·76	
Mean	0·0981	64·81	−1·935

The parameters were established for females only, because the initial number N_0, was considered to be a function of a number of ovaries. From the parameters averaged for the three year-classes the specific annual growth rates were calculated.

Figure 1 shows the trend in $(G - M^*)$ with age, and at the age of 16 $(G - M^*) = 0$; i.e. the critical age, $T, = 16$. It is a provisional estimate which cannot be established more firmly until the nature of the apparent growth increase has been understood.

During the sixties, an average value of fishing mortality in the adult age groups of females was obtained. Total mortality was estimated from the ratio of numbers per 100 ton-hours fishing averaged for the six years in successive ages in the catch curve. The same data were averaged by moving means of threes and, for the ages 5–16, density-dependent mortality was subtracted to give an estimated F of 0·215. This value corresponds quite well with an estimate made by my colleague Dr. R. C. A. Bannister using virtual population analysis. The number at the critical age when $F = 0·215$ is $2 \cdot \exp(-F) = 1·613$; that is, the value of 2 is reached at thirteen. This does not mean that the critical age has shifted from sixteen to thir-
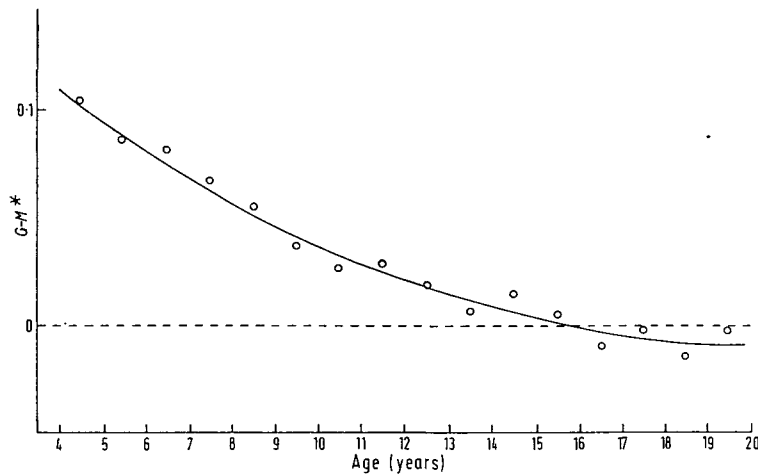
Figure 1. The critical age in plaice, at which $(G-M^*) = 0$.

teen, because neither G nor M^* have changed; under exploitation, the stock replaces itself at a lower level.

The trend in N_t from hatching to the critical age can be established if the initial mortality is known. The loss rates of the plaice larvae are known: 80%/month or 99·20%/3 months (the estimate of 80%/month is based on the observations for ninety days for the first three months of larval life; Harding and Talbot, 1973) which must include both components, density-dependent and density-independent.

$N_{30}/N_0 = 0·2 = 1/(1 + 30M_0) \therefore M_0 = 0·133$
then $M_0 = N_0 - 2e^{-F}/2e^{-F} \times 13 \therefore N_0 = 1026·5$

N_t can be calculated for any number of ages. Figure 2 shows the trend in numbers with age, exploited at $F = 0·215$, assuming that $M_0 = 0·133$. The mortality during the first quarter of life is 80%/month, as given above. The mortality rates of 0-group fish of 40%/month at recruitment (in June) or 10–20%/month during the following winter are marked on the figure; these estimates of 0-group mortality are summarized from recent work by Lockwood (in preparation). The mean peak date of spawning is 19 January (Cushing, 1969), so the time of first feeding is probably in early March. If the initial mortality of 80%/month lasts a month to early April, it is reduced to 38%/month by June, when the little fish are recruiting to the beach. The adult natural mortality is taken from the loss rates of the trans-wartime year-classes (Beverton and Holt, 1957); between the ages of 5, 6 or 7 before the Second World War to 13, 14 or 15 after it. The mortality rate estimated in this way was 0·1 although Beverton (1964) in a later analysis of the data suggested that $M \, ♀ = 0·08$ and $M \, ♂ = 0·12$. For the ages
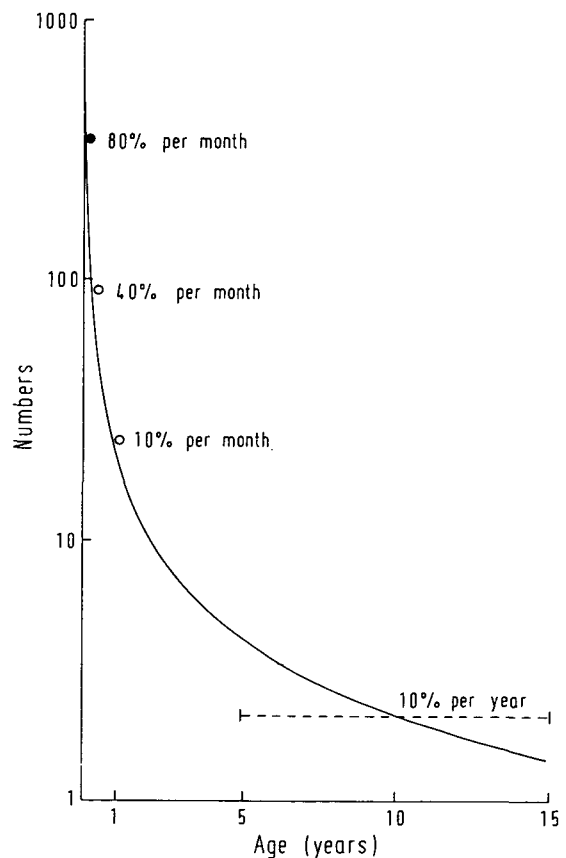

Figure 2. The trend in density-dependent mortality with age, assuming a larval mortality of 80%/month; the 0-group mortalities of 40%/month at 4 or 5 months and of 10%/month in the first winter, and the adult mortality of 10%/year are predicted.

5 to 15 it can be shown that the average mortality rate calculated by the curve given in Figure 2 is 9·7 %/ year. Given the initial larval mortality rate, the trend of mortality with age from larval life to the critical age can be fairly well simulated.

The senescent mortality of the plaice

In well exploited populations, the natural mortality (M) of adult fishes is often given a fixed value because the differences, if any, will be small as compared with the fishing mortality (F) in the abundant age groups. In unexploited or lightly exploited stocks, the assumption might not hold (if $M \geqq F$). Further, such a population with a mortality rate that declines with age lived for a very long time, perhaps longer than it need do. Gompertz (1825) suggested that the mortality of adult animals should increase exponentially with age in order to terminate the numbers in age. Beverton (1964) drew attention to the Gompertz law and expressed it in the following form:

$$N_t = N_1 \exp - [\exp(m_0 + m_1 t)],$$

where N is an initial number in stock density, for example at the critical age; N_t is a number in stock density at a later age; m_0 is the natural mortality rate at the critical age; and m_1 is the rate at which mortality increased with age.

Since 1963, otoliths of the plaice population in the southern North Sea sampled at Lowestoft have been examined by Christensen's (1964) burning method, with the result that ages are determined routinely to the 21st year. I am grateful to Dr R. C. A. Bannister for making the otolith samples available to me and to Mr T. Williams, who made detailed age determinations up to the age of 35. The samples were taken from the year-classes 1933–50.

The numbers per 100 hours' fishing of female plaice between 1964 and 1969 were first averaged by years to form a "catch curve". From the ages of 5 to 31, the total mortality was estimated in two ways, first, from the numbers per 100 hours' fishing, and secondly, from the same data averaged by moving means. From these estimates, the density-dependent mortality was subtracted for the age groups 5–16. By this means it was estimated that $F = 0\cdot215$ in the ages 5–16 and $m_0 = 0\cdot078$ at age 16. A "catch curve" does not provide good estimates of total mortality because it can conceal a trend in time. The "catch curve" was used because to apply other methods completely would not be possible until 1992. Any estimate of the trends of mortality in the older age groups would be biased by their mortality history in

earlier years. In general the trend in mortality on the plaice population has been declining. The oldest year-classes sampled entered the fishery in 1938 when F (on both sexes) was 0·73 (Beverton and Holt, 1957). Then followed a period of no fishing during the war. Subsequently the value of $F \simeq 0\cdot5$ (Gulland, 1968) declined during the fifties and perhaps it fell further during the sixties. The mortality of females might have always been lower than that on both sexes combined. The natural mortality of the plaice was well estimated from the trans-wartime year-classes (Beverton and Holt, 1957; Beverton, 1964): $M = 0\cdot1$. The trend of mortality might have been as follows:

	F	Z
1938–9	0·7	0·8
1940–5	0·0	0·1
1946–54	0·5	0·6
1955–63	0·3	0·4
1964–70	0·2	0·3

It is assumed that the difference between the sexes in mortality tends to decrease with increasing fishing; however, it is possible that the downward trend in mortality on the females is a little overestimated. For a constant number of recruits, stock densities were calculated with this set of mortalities for the year-classes 1943–54, summed as a catch curve in the years 1964–70. The average mortality was 0·42, whereas the "catch curve" mortality was 0·58, so mortality was overestimated by the catch curve. Earlier year-classes were subject to no mortality during the war and then the "catch curve" mortality would underestimate the true mortality. In fact the
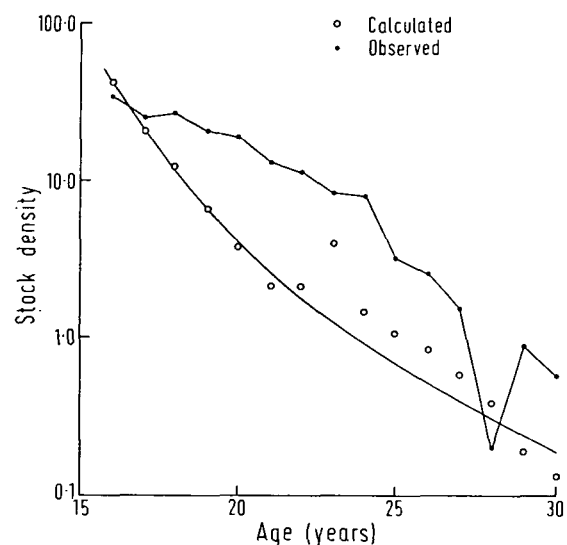

Figure 3. The calculated catch curve with no fishing mortality during the war and a declining mortality after it (O), contrasted with the observed catch curve (●).

"catch curve" mortality for all age groups was 0·26, and the average mortality was 0·38, so the catch curve underestimates mortality in the age groups 16 to 31 in the period under investigation. Figure 3 shows the observed catch curve and the one calculated by the method given above. The calculated one tends to overestimate mortality between the ages 16 to 21, but to underestimate it overall, with the effect that the shape of the curve is concave; the concavity is a combined result of declining mortality in the post-war years and of no fishing mortality during the war itself. If the decline in mortality is a little overestimated the initial slope is a little too high, but the effect would be to reduce the concavity to some extent; the overall underestimate of mortality from 16 to 31 would remain, although it would be reduced a little. The observed catch curve is convex, as if a senescent mortality did occur. The contrast between the two is enough to justify fitting Beverton's (1963) equation; the study of the possible nature of the catch curve shows that any estimate of fishing mortality used between the ages of 16 and 31 is an underestimate by as much as 50%. Further, it is assumed that fishing mortality is constant in the catch curve and so the changes in time have to be incorporated in an average figure.

Beverton's equation was used as follows:

$$N_t/N_1 = \exp - [Ft + \exp (m_0 + m_1 t) - \exp m_0].$$

With $N_1 = 34·3$, $N_t = 0·5$, $t = 15$, $m_0 = 0·078$, m_1 was calculated for a range of values of F (= 0·0, 0·10, 0·15, 0·20). Then the curve was fitted to the observed data between the ages of 16 and 31. The calculation was made in this form because at the lower limit, when $t = 0$, $N_0 = N_0 \exp(- [\exp(m_0)])$. The observations are not independent of each other, so a statistical comparison between the calculated curves and the observations cannot be made. An attempt was made, using differences from the observations, but the variance was too high and statistical tests had to be abandoned.

Figure 4 shows the observations between the ages of 16 and 31 and curves of senescent mortality calculated at different levels of fishing mortality. The curves with $F = 0·0$ and $F = 0·2$ do not fit the data at all. The observations appear to be grouped in two parts, in ages 16–24 and in ages 25–31; the first period would be fitted by $F < 0·10$ and the second by $F = 0·10$–$0·15$. Hence it is likely that there was a change in mortality in the catch curve. It will be recalled that the catch curve probably underestimates the fishing mortality by about 50%. Hence a true average value might be between 0·15 and 0·21. The point of evidence is that the observations in the form of a catch curve cannot be described by the trends in mortality
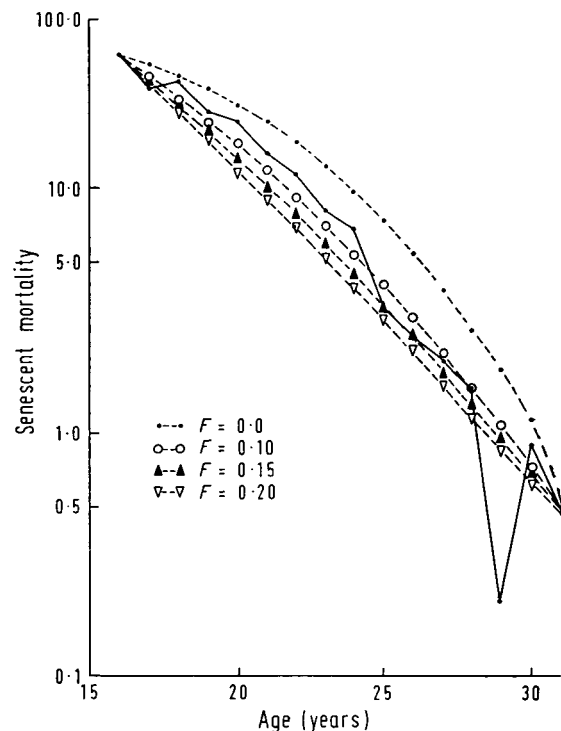

Figure 4. The observed catch curve fitted with Beverton's 1963 equation with different values of F.

in the cohorts that contribute to them, and that they can be described by a form of senescent mortality. At $F = 0·1$, $m_1 = 0·0855$, and at $F = 0·15$, $m_1 = 0·0728$ and it would appear that either value would be applicable; the values of fishing mortality are underestimated, and perhaps with better data obtained in future years higher values of m_1 might emerge.

Discussion

In the plaice the trend in natural mortality with age from the time of first feeding to the critical age, and from then to the age at which the cohort is extinguished, is of the form described by Deevey for a number of animals. If the mechanism can be extended to other fishes, it is a useful accident that the specific mortality rate is the same in the adult age groups, so long as the initial number is large enough. Further, because density-dependent growth is absent in the adult age groups (except in the youngest ages of the Pacific halibut; Southward, 1967), the critical age can be determined easily.

Figure 5 shows the trends in specific mortality rate and specific growth rates (by quarter years) for the
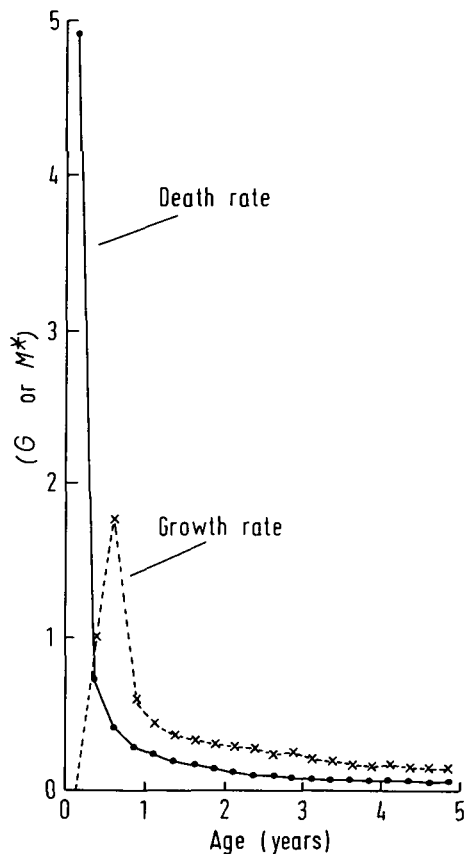
Figure 5. The trend in G and M^* by quarters during the first four years of life.

dependent function of age. The density dependence needs a period of time in which to develop, as in Beverton and Holt's formulation, which itself followed an idea originated by Ricker and Foerster (1948). The extension in time from a critical period to most of the young and adult life may appear unwarrantable, but in terms of the reduction of numbers, the extension may be so small as to be almost trivial. The expression used here gives the initial number and so the initial mortality is stock-dependent, but the subsequent curve in age describes the average course of both stock-dependent and density-dependent processes.

There is a sense in which it is preferable to consider density-dependent mortality as predominant to density-independent mortality if not numerically so. The loss in numbers in juvenile life is then not merely a waste, but is a continous and fine control of recruitment. The density-dependent processes are modulated all the time by the availability of food, in the way in which Jones (1973), and Cushing and Harris (1973) have suggested. In this view, the stock-dependent processes which operate from generation to generation are conservative, but the density-dependent processes which operate in juvenile life are exploratory. The consequence would be that the carrying capacity of the environment, as the availability of food, is exploited continously by density-dependent processes. Such a structure is to me a much more likely one than that supposed in a massive loss of larvae by environmental effects. It is an important point to realize that such a small and temporary loss would be modulated in a density-dependent manner. Thus, variability in food or more generally in the environment, generates the capacity of the cohort to exploit it.

first four or five years of life of the plaice. The mortality rates follow the type of trend shown in Figure 2, but the growth rates increase sharply on the nursery ground presumably because food is plentiful and predators relatively few. During life on the nursery ground the specific growth rate becomes greater and remains so until the critical age, after which senescence may supervene with a mortality rate greater than growth rate. The period of excess growth is that in which fecundity is built up, and, in an average condition, fecundity and egg production in the virgin stock are determined by the growth rate. Variability in stock produces variability in egg production and hence the subsequent density-dependent processes. Whereas individual fishes grow in order to delay death, the growth of fish in the population has the purpose of generating as much fecundity as possible and to increase the capacity of the stock to stabilize itself.

The central thesis of this paper is that natural mortality can be provisionally described as a density-

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