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Sources of errors in and limitations of Virtual Population Analysis (Cohort analysis)

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1. Introduction.

The Virtual Population Analysis or Cohort analysis is extensively used in stock assessment both within ICES and other scientific bodies. It is an extremely useful technique for estimating past values of fishing mortalities and stock sizes. These part values may in several ways be utilized to get indications of the present state of the stock and the prospects for the coming years. Because of the extensive use of the method it is however, important to know the limitations of it and the various sources of errors. Contributions on this was given by POPE (1971) and AGGER, P., BOËTIUS, I. and LASSEN, H. (1971). In this paper some further aspects will be discussed.

2. Clarifications of terms used.

The term Virtual Population was introduced by FRY (1949) and defined as the sum of the catches of a yearclass which has passed through the fishery. GULLAND (1965) developed a way of estimating population and fishing mortality by a stepwise correction of the virtual population.

Identical results can be obtained without involving the virtual population at all. Given the two equations for catch of a yearclass in year i and stock size in year i and i + 1

$$C_i = N_i \cdot \frac{F_i}{F_i+M} \left(1 - e^{-(F_i+M)}\right)$$

$$N_{i+1} = N_i \quad e^{-(F_i+M)}$$

F_i and N_i may be found either by iteration or by reference to tables if N_{i+1}, C_i and M are known. Having estimated F_i and N_i, one can then go back to year i - 1 and so on. For the last year (the starting year for the analysis) one has to assume a value for N or calculate N from an assumed or estimated value of F.

It is this method which at present is called Virtual Population Analysis (VPA). It is essentially nothing more than using the BEVERTON and HOLT (1957) equations given above backwards instead of forwards, and it makes no use of FRY's Virtual Population. The method was outlined by MURPHY (MURPHY 1965). Unfortunately it has caused some confusion that the method now is called Virtual Population Analysis. The term Cohort analysis was used by POPE (1971) for a method similar to VPA, the only difference being that the approximate formula

$$N_i = C_i \; e^{M/2} + N_{i+1} \; e^{M}$$

is used instead of solving the two simultaneous equations given above. In this paper the term VPA will be used in the present common way.

3. Effects of wrong starting value for N(F) and sampling errors of the catch data.

These aspects were discussed by POPE (1971) and will not be further discussed in any detail in this paper. POPE showed that such errors converge to fairly small values as one calculate the strength of a yearclass backwards. It should be stressed that the relative error in N(F) in year i when starting with a wrong value of N(F) in year t is not determined by the size of the time period between year i and year t but by the cumulative fishing mortality during the period. The estimates converge rapidly towards the true values when the fishing mortality is high. With low fishing mortalities the convergence is slower and in the extreme case when $\frac{F}{M}$ approach O there will be almost no convergence as one calculate backwards year for year.

4. Effects of errors in the natural mortality (M).
(i) Constant natural mortality.

One common way of estimating the starting value of fishing mortality is to estimate Z_t from catch per unit of effort data and then calculate F_t by $\hat{F}_t = \hat{Z}_t - \hat{M}$.[1] The estimate of Z will be independent of any assumption about natural mortality. It will therefore be assumed here that the final $\hat{Z}_t$ is correct.

Then $\hat{F}_t = \hat{Z}_t - \hat{M}$ will be in the same absolute error as $\hat{M}$, but with opposite sign for the error.

$$\hat{F}_t - F_t = M - \hat{M}.$$

From the equation

$$C_t = N_t \cdot \frac{F_t}{Z_t} \left(1 - e^{-Z_t}\right)$$

it follows that

$$\frac{N_t F_t}{Z_t} \left(1 - e^{-Z_t}\right) = \frac{\hat{N}_t \hat{F}_t}{Z_t} \left(1 - e^{-Z_t}\right) \qquad \text{(C is given)}$$

i.e.

$$N_t F_t = \hat{N}_t \hat{F}_t$$

$$\frac{\hat{N}_t}{N_t} = \frac{F_t}{\hat{F}_t} = \frac{Z_t - M}{Z_t - \hat{M}}$$

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1) A $\wedge$ denotes an estimated or assumed value.

If Z is constant from year to year, the last equation will be valid for all years when one calculate the stock backwards by VPA. Z_i ($i < t$) and the relative changes in stock size from year to year will be correctly estimated by VPA, but stock size will be over- or underestimated when M is over- or underestimated, and the relative error is given by the equation above. The error in $\hat{F}$ will be constant and equal to $M - \hat{M}$.

If Z varies from year to year errors in $\hat{M}$ also generally will give errors in $\hat{Z}_i$ and therefore errors in estimated relative changes in stock size. However, the errors in $\hat{Z}_i$ will be fairly small if the fluctuations in Z_i are moderate. This may be illustrated by the following example.

Assume F_i fluctuates randomly from year to year on a yearclass as shown in Fig. 1, where F_i varies between 0.42 and 0.83, and assume M = 0.2. The two dotted lines in Fig. 1 show estimated F-values from VPA assuming M = 0.1 and M = 0.3, using the catches corresponding to M = 0.2 and the true total mortality for the last year when estimating starting values for N_t in the VPA. In Fig. 2 are plotted estimated and true total mortalities.

As expected M = 0.1 gives too high F-values and M = 0.3 gives too low F-values. The differences between estimated and true Z-values are small, the biggest differences (ca. 0.04) occurs when the change in Z (F) from one year to another is large. For both M = 0.1 and M = 0.3 the estimated Z-values fluctuate around a mean value approximately equal to the true mean. A low M(0.1) tends to overestimate fluctuations in Z and thereby overestimate F to a smaller extent when F is low than when F is high, while a high M(0.3) tends to underestimate fluctuations in Z (F) and thereby underestimate F to a smaller extent when F is low than when F is high. This has one important consequence: If the estimated F-values using wrong M are plotted against fishing effort, the wrong M will not generally cause a significant intercept of the regression line on the F-axis which then could indicate that a wrong M was used. This is illustrated in Fig. 3 where true F-values (effort) are plotted against estimated F-values using M = 0.1 instead of the correct M = 0.2. (In order to get a wide range of F-values the deviations of the individual true F's from their mean were made twice as big as in Fig. 1. The $\hat{F}$-values corresponding to M = 0.1 were then estimated by the method used for Fig. 1 - Fig. 2). The estimated regression line has an intercept on the F-axis of only 0.022 while the error in M is - 0.1.

(ii) Natural mortality varies

If M varies randomly from year to year, this will cause a component of random fluctuations in the total mortality Z. These fluctuations will disappear almost completely in the VPA estimates if a constant natural mortality $\hat{M}$ is assumed. Disregarding errors caused by wrong starting values in the VPA, the estimated F-values ($\hat{F}$) generally will follow the same trend as the true F's. The level may be different depending on the relation between $\hat{M}$ and the mean value $\overline{M}$ which the true natural mortality fluctuates around.

The effects of random fluctuations in M are illustrated in Fig. 4. M varies around a mean value of 0.2 with lowest and highest value being 0.12 and 0.30 respectively (Fig. 4a). Assuming a constant fishing mortality of 0.2, the total mortality Z fluctuates to the same extent as M(Z= M + 0.2). When a constant $\hat{M}$ = 0.2 was assumed in a VPA (using catches corresponding to true M and F, and assuming $\hat{Z}$ = Z for the last year), the estimated $\hat{F}$-values were nearly constant with a maximum value of 0.212 and a minimum value of 0.19. Thus, the highest relative error in $\hat{F}$ was only ca. 6% (Fig. 4b), but the fluctuations in Z almost completely disappeared (Fig. 4a). The highest relative error in stock size estimates ($\hat{N}_i$) was also only about 6% (Fig. 4b).

In conclusion, errors in $\hat{F}_i$ and $\hat{N}_i$ from VPA caused by random fluctuations in M are likely to be small when M fluctuates moderately. The largest errors will appear in the estimated total mortalities $\hat{Z}_i$.

A trend in M with time or age will cause trends in the errors in $\hat{N}_i$, $\hat{F}_i$ and $\hat{Z}_i$ with time or age if a constant M is assumed in a VPA.

For illustration an example was constructed where M varied with age (i) of a yearclass according to the equation

$$M_{i+1} = M_i (1 - (M_i - 0.1)), \quad M_1 = 0.3 \quad \text{(Fig. 5a)}$$

M approaches the asymptotic value 0.1 as i increases (for very high i's a more realistic assumption would probably be that M started to increase again).

True values of N_i, F_i and Z_i were compared with estimated values from VPA (using catches corresponding to true values, and assuming $\hat{Z} = Z$ for the oldest age) for two constant F-values, F = 0.2 and F = 0.6. Two different constant $\hat{M}$'s, $\hat{M} = 0.1$ and $\hat{M} = 0.2$, was used in VPA, and this resulted in four VPA's, two for F = 0.2 (Fig. 5b) and two for F = 0.6 (Fig. 5c).

Generally, the errors in $\hat{N}_i$ and $\hat{Z}_i$, and the relative errors in $\hat{F}_i$, decreased when F increased from 0.2 to 0.6. As F increases a larger portion of the total mortality is comprised by F and therefore the errors created by wrong M-values in the VPA's decrease.

For both F-values $\hat{Z}$ underestimated Z and the errors in $\hat{Z}$ increased as i (age) decreased both for M = 0.1 and M = 0.2. That this was the case also for M = 0.2. (which is in between the range of the true M-values and almost equal to the true M for age 3) illustrates the fact that it is not the differences $\hat{M}_i - M_i$ themselves which mainly cause the errors in $\hat{Z}_i$, but the changes with age in these differences created by changes in M_i (or Z_i, cf. section 4(i)).

The $\hat{Z}_i$-values were a little smaller and $\hat{Z}_i - Z_i$ a little larger for M = 0.2 than for M = 0.1 (for F = 0.6 the differences were insignificant) M = 0.2 thus created the largest errors in $\hat{Z}_i$ even if M = 0.2 is in between the actual range of the true M_i's while M = 0.1 is outside this range. This illustrates the point mentioned in section 4(i) that changes in $\hat{Z}_i$ from year to year decreases when $\hat{M}$ increases. As Z_i continuously increases with decreasing age, a high constant $\hat{M}$ gives in this case larger errors in Z_i than a low one, even if the higher $\hat{M}$ is nearer the true M_i's. In fact trials with other constant $\hat{M}$'s showed that $\hat{M} = 0$ gave the best fit as far as $\hat{Z}_i$ was concerned.

For both F-values the estimated $\hat{F}_i$ (Fig. 5b - 5c) increased with decreasing i. Thus, increasing natural mortality showed up as increasing fishing mortality in VPA. As expected, for the older ages $M = 0.1$ gave the smallest errors in F_i, while $M = 0.2$ gave the best fit for the youngest ages. The same was the case for N_i (Fig. 5b - 5c). $\hat{M} = 0.1$ strongly underestimated N_1 for both F-values, while $M = 0.2$ slightly overestimated N_1 when $F = 0.2$ and slightly underestimated N_1 when $F = 0.6$ ($F = 0.6$ implies that a larger portion of the catch is taken when the yearclass is 1-3 years old and has a natural mortality even higher than the value 0.2, see Fig. 5a).

The strong underestimation of N_1 when the low $\hat{M} = 0.1$ was assumed has one interesting consequence: If in a certain stock the natural mortality is at a rather low and constant level for "normal" yearclasses but is higher at young ages for especially strong yearclasses, the VPA technique using a constant M will underestimate the strength of strong yearclasses at young ages relative to weaker yearclasses. For several stocks (e.g. North Sea Herring (ANON 1975)) it has been observed that when the regression of VPA-strength of a yearclass against abundance indices from young fish trawl surveys are calculated, one gets a significant positive intersept on the VPA-axis. This may of course be a result of bias in the abundance indices from trawl surveys. From what is said above it follows, however, that this intercept also may be explained by a bias in the VPA results. This is illustrated in Fig. 6. It is there assumed that abundance indices from young fish surveys give unbiased relative strength of a yearclass at age 1. If a "normal" yearclass has a constant natural mortality of 0.1 but a yearclass three times stronger at age 1 has a natural mortality given by Fig. 5a, a plot of VPA strength assuming $\hat{M} = 0.1$ against the young fish survey indices would give the dotted line in Fig. 6, which has a large intercept at the VPA axis. (It is assumed that both yearclasses were fished at an $F = 0.2$ from age 1 onwards).

5. Effects of seasonal variations in F and M.

The Beverton and Holst's catch equation

$$C_t = \frac{N_t F_t}{Z_t} (1 - e^{-Z_t})$$

is based on evenly distributed fishing and natural mortality throughout the year. If this is not the case, one will make errors both in a prognoses calculating the stock size N_{i+1} corresponding to given N_i and C_i, and in a VPA calculating N_i corresponding to given N_{i+1} and C_i. The errors when calculating forwards (prognoses) and backwards (VPA) will, however, cancel out in the sense that when starting with the wrong $\hat{N}_{i+1}$ from the prognoses in the VPA, you will get back to the "true" N_i.

The size of the errors involved in a VPA is illustrated in Fig. 7. It is there assumed that all catch is taken in the first or last quarter of the year. The relative errors in $\hat{N}_{i-1}$ starting with correct N_i are plotted against annual F (correct value taking into account the seasonal distribution of the catch) for different values of the natural mortality.

The errors are generally small and negligible. One can get rid of these errors by carrying out the VPA on smaller time units than a year (if it is possible to give the catch on smaller time units). If this is done one should, however, also carry out any prognoses on these smaller time units, otherwise the errors in the prognoses may even increase because of the above mentioned "cancel out" nature of the errors.

In POPE's (1971) approximate formula

$$N_i = C_i \, e^{M/2} + N_{i+1} \, e^{M}$$

it is implicit assumed that fish of a certain year class caught during year i have a mean living time of half a year in year i. If F and M are evenly distributed over the year this mean living time will, however, be less than half a year because there is a steadily decreasing number of fish in the sea, and therefore a steadily decreasing number of fish in the catch, during the year. The mean living time will decrease with increasing F and M.

The true relation between N_i and N_{i+1} may be written as

$$N_i = C_i e^{kM} + N_{i+1} e^{M}$$

where k is a function of F and M. k may be interpreted as the above mentioned mean living time. In Fig. 8 is k plotted against F for various values of M. Instead of using POPE's approximate formula in the cohort analysis one may use the equation given above, assuming a value of k which corresponds approximately to the actual levels of F and M (if F do not vary too much from year to year).

If the fishery is typical seasonal it may be better to use the equation given above instead of the Beverton and Holts equations. One may then either define the beginning of the year as the main fishing season and put k = 0, or define the beginning of the year as 1 January and put k equal to the time period between 1 January and the main fishing season.

If fishing and natural mortality are evenly distributed over the year, a VPA on a monthly or quarterly basis will give exactly the same results as a VPA on an annual basis (if one starts with the same input stock size for the last year). The errors in $\hat{F}_i$ and $\hat{N}_i$ when calculating a yearclass backwards by VPA, caused by wrong starting values, will not decrease more rapidly when the number of time intervals are increased by using a smaller time unit. It is the cumulative fishing mortality, not the number of time units, which determines the rate of convergence towards the true values.

6. Stock migration.

One of the largest sources of errors in the VPA technique lies in the implicit assumption made when carrying out a VPA on a stock area A that a fish caught in this area at age x also was in the area at any age $y < x$.

If a yearclass from a certain age on continuously migrate from an area A to an area B at a constant instantaneous emigration rate E, a VPA for area A will give correct values for N_i and F_i if E is included in the natural mortality for area A, i. e.

$$M'_A = M_A + E$$

where M_A is the "true" natural mortality and M'_A is the "appearant" natural mortality used in the VPA.

For area B, however, the situation will be much more complicated as far as the VPA is concerned. The number of fish of a certain year-class which immigrates to the area at any time is determined by the number of fish left of the yearclass in area A, i. e.

$$dN_{AB} = EN_A \, dt$$

where N_{AB} is the number of fish which migrates into are B from area A. Therefore, one can not adjust the VPA for area B simply by making an adjustment of the natural mortality as it could be done for area A.

Let

F_A = instantaneous fishing mortality in area A.

F_B = instantaneous fishing mortality in area B.

N_A = the number of fish in a certain yearclass at the beginning of the year in area A.

N_B = the number of fish in the yearclass at the beginning of the year in area B.

C_A = catch (in number) of the yearclass throughout the year in area A

C_B = catch (in number) of the yearclass throughout the year in area B.

E = instantaneous emigration rate from area A to area B.

M = natural mortality (for simplicity it is assumed that M is the same for area A and area B. One could, however, easily introduce separate natural mortalities for area A and area B in the equations developed below).

At any time t within the year the number of fish in the yearclass in area A is given by

$$(1) \quad N_{A,t} = N_A\, e^{-(M + E + F_A)\, t}$$

and setting $t = 1$ gives the number at the beginning of next year. The catch during the year in area A is then given by

$$(2) \quad C_A = F_A\, N_A \int_0^1 e^{-(M + E + F_A)\, t}\, dt = \frac{N_A \cdot F_A}{F_A + M + E}\left(1 - e^{-(F_A + M + E)}\right)$$

Equations (1) and (2) are simply the common Beverton and Holt's equations with M substituted by M+E. Accordingly a VPA may be run for area A by substituting M by M+E in the VPA formulas.

The number of fish which migrates into area B in any infinitesimal time interval dt_1 is given by

$$dN_{AB,t_1} = EN_A\, e^{-(M+E+F_A)\, t_1}\, dt_1$$

Of these

$$dN_{AB,t_1} \cdot e^{-(M+F_B)\,(t - t_1)}$$

survives until time t ($t > t_1$). Therefore, the number of fish in area B at time t which have emigrated from are A during the year is given by

$$N_{AB,t} = \int_0^t EN_A\, e^{-(M+E+F_A)\, t_1}\, e^{-(M+F_B)(t - t_1)}\, dt_1$$

$$= EN_A\, e^{-(M+F_B)\, t} \int_0^t e^{-(M+E+F_A)\, t_1}\, e^{(M+F_B)\, t_1}\, dt_1$$

$$= EN_A\, e^{-(M+F_B)\, t} \int_0^t e^{-(E+F_A - F_B)\, t_1}\, dt_1$$

$$= \frac{EN_A}{E+F_A-F_B} \left(e^{-(M+F_B)t} - e^{-(M+E+F_A)t}\right)$$

In addition

$$N_B \; e^{-(M+F_B)t}$$

of the fish which were in area B at the beginning of the year will have survived until time t.

Thus, the number of fish in area B at time t is given by

$$(3) \quad N_{B,t} = N_B \, e^{-(M+F_B)t} + \frac{EN_A}{E+F_A-F_B} \left(e^{-(M+F_B)t} - e^{-(M+E+F_A)t}\right)$$

and setting $t = 1$ one gets the number at the beginning of the next year. Equation (3) shows that the resultant total "mortality"

$$\left(- \ln \frac{N_{i+1}}{N_i} \right)$$

throughout the year in area B is given by

$$- \ln \left(e^{-(M+F_B)} + \frac{N_A}{N_B} \; \frac{E}{E+F_A - F_B} \left(e^{-(M+F_B)} - e^{-(M+E+F_A)}\right)\right)$$

For high values of E and $\frac{N_A}{N_B}$, and low values of F_B, this "mortality" may become negative.

The catch throughout the year in area B is given by

$$C_B = \int_0^1 F_B \, N_{B,t} \, dt$$

which, by using equation (3), is equal to

$$C_B = \int_0^1 F_B \left(N_B e^{-(M+F_B)t} + \frac{EN_A}{E+F_A-F_B} \left(e^{-(M+F_B)t} - e^{-(M+E+F_A)t}\right)\right) dt$$

The solution of this integral may be written as

$$(4) \quad C_B = \frac{F_B}{M+F_B} \left(N_B + \frac{EN_A}{E+F_A-F_B}\right) \left(1 - e^{-(M+F_B)}\right)$$

$$- \frac{F_B}{M+E+F_A} \cdot \frac{EN_A}{E+F_A-F_B} \left(1 - e^{-(M+E+F_A)}\right)$$

As explained above, the usual VPA technique may be used to calculate stock sizes and fishing mortalities backwards in area A if E is known, setting M' = M+E. Knowing then F_A and N_A, it is possible to use equations (3) and (4) in a way similar to the VPA technique to calculate N_B and F_B backwards year for year because the only unknown, knowing $N_{B,i+1}$ and $C_{B,i}$ will be $N_{B,i}$ and $F_{B,i}$. This has to be done by developing a program which solves the simultaneous equations (3) and (4) by interation, or by utilizing tables which, however, would be much more complicated than in the usual VPA. This topic will not be discussed further in the present paper.

Equations (1) to (4) make it possible to study how the results of a VPA, which do not take any account of the migration, would depart from the true values of stock sizes and fishing mortalities. For illustration the following values for the parameters were chosen:

$M = 0.2$

$E = 0$ for age-groups 1 and 2, $E = 0.2$ for 3 years old and older fish

$F_A = 0.3$ $F_B = 0.6$

$N_{A,\text{ age }1} = 1500$ $N_{B,\text{ age }1} = 3000$

Catches and stock sizes of the different age-groups were calculated for each area separately using the equations (1) to (4). Catches and stock sizes in the two areas were then summed to get catches and stock sizes for the areas combined. For each area and the areas combined total "mortality" on age group i (Z_i) was calculated as $- \ln N_{i+1}/N_i$. The fishing mortality on age group i (F_i) for the areas combined was calculated as $Z_i - M = Z_i - 0.2$.

Using then the calculated catches three different VPA's were run, one for each of the areas and one for the areas combined. The true value was chosen as starting value for the stock size of the oldest age-group (the 9 years old). In addition one VPA was run for each area, using a starting stock size calculated from the true total "mortality" and catches of 8 years old. In all runs a natural mortality of 0.2 was used. The results are shown in Fig. 9a - c.

As expected the combined VPA gave results almost exactly equal to the true values (Fig. 9a). Some negligible differences in the decimales have the following explanation: In VPA it is assumed that fishing mortality is evenly distributed over the year (cf. section 5). This is in the example not the case for the areas combined. The fishing mortality gradually changes according to changes in the ratio $N_{B,t}/N_{A,t}$. For ages 1 and 2 $N_{B,t}/N_{A,t}$ decreases during the year because of higher total mortality in area B than in area A, and as a result F gradually decreases, because $F_B > F_A$. VPA therefore slightly overestimates N_i/N_{i+1} for these age groups (cf. section 5). For the older age-groups the contrary is true because of the continuous migration from area A to area B which results in a gradual increase in the ratio $N_{B,t}/N_{A,t}$ during the year [1].

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[1] It was demonstrated that by dividing the year into 5 equal parts the VPA analysis gave results closer to the true values, which confirms this explanation. For example, on an annal basis

$$\frac{\hat{N}_3}{\hat{N}_4} - \frac{N_3}{N_4} = - 0.000368$$

while by dividing the year into 5 parts when carrying out the VPA

$$\frac{\hat{N}_3}{\hat{N}_4} - \frac{N_3}{N_4} = - 0.000027$$

The results of the separate VPA's showed that

$$\hat{N}_A + \hat{N}_B \approx N_A + N_B$$

This is also what should be expected as VPA essentially estimates stock size of a yearclass by summing the catches of the different age groups, correcting the catches of each age group for the natural mortality this age group has experienced. In the constructed example M is equal in the two areas and it therefore should not matter what area the catch is taken in when one correct for natural mortality. However, for a given M, the relation between stock sizes in two successive years may be written as (cf. section 5)

$$N_i = C_i\, e^{kM} + N_{i+1}\, e^{M}$$

k will depend on F_i, or on how the catch is distributed over the year. k will be correctly estimated in the VPA if fishing mortality is evenly distributed over the year and there is no migration from or to the area during the year. However, in our example, the migration will disturb this in the separate VPA's, and therefore $N_A + N_B$ will not be exactly equal to $\hat{N}_A + \hat{N}_B$.

The VPA for area A (Fig. 9b) underestimates stock size and overestimates fishing mortality because the natural mortality used does not include emigration and therefore is too low. The estimated total mortality $\hat{Z}_A$ gradually approaches the correct value as the yearclass is backcalculated until age 3. For age groups 2 and 1 the true mortality Z_A decreases from 0.7 to 0.5 because these age groups do not emigrate, and $\hat{Z}_A$ strongly overestimates Z_A. If one instead of assuming $\hat{N}_{A,9} = N_{A,9}$ in the VPA put $\hat{Z}_{A,8} = Z_{A,8}$, the VPA correctly estimate Z for age-groups 3-8, but constantly overestimate F to 0.5 compared with the true value of 0.3. This is in agreement with what was said in section 4(i) concerning the case when Z is constant, $\hat{Z}_{\text{last year}}$ correct, but M is wrong in the VPA.

As expected, a VPA assuming M = 0.4 (M = 0.2 + E) for age-groups 3-8 and M = 0.2 for ages 1 and 2 gave results identical to the true values.

The comparison of true values with VPA results for area B (Fig. 9c) is the more interesting part of the exercise. The first interesting feature is that Z_B is less than F_B for ages 3-8, the difference decreasing with age. This means that migration into the area more than compencates natural mortality, or that the resultant "natural" mortality is negative. A VPA assuming a constant (positive) natural mortality will then of course give completely wrong results both for N_B, F_B and Z_B. $\hat{N}_B$ strongly overestimates N_B, and the relative overestimation increases with decreasing age (until age 3). $\hat{Z}_B$ strongly overestimates Z_B (for age 3-8), and $\hat{F}_B$ strongly underestimates F_B. $\hat{Z}_B$ and $\hat{F}_B$ strongly decreases with age until age 3, giving an $\hat{F}_B$ for age group 3 of 0.29 against a true value of 0.6[1]. By assuming $\hat{Z}_8 = Z_8$ instead of $\hat{N}_9 = N_9$, the $\hat{Z}_B$ will be nearer the true value for the older age groups but the errors in $\hat{F}_B$ will increase.

As long as a constant M is assumed in the VPA, the VPA will give a completely wrong picture of the real situation, and the only way to solve the problem is to try to take account of the immigration by utilizing the equations (3) - (4), assuming N_A and F_A already have been estimated by VPA using equations (1) - (2).

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1) An example of a VPA which shows a decreasing F with age (in age groups which normally should be fully recruited to the fishery) is found in Report of the North-Western Working Group (ANON 1976). The Working Group explained the low estimated fishing mortality on age-groups 4-6 for some yearclasses of cod at Iceland by immigration from East and southern West Greenland.

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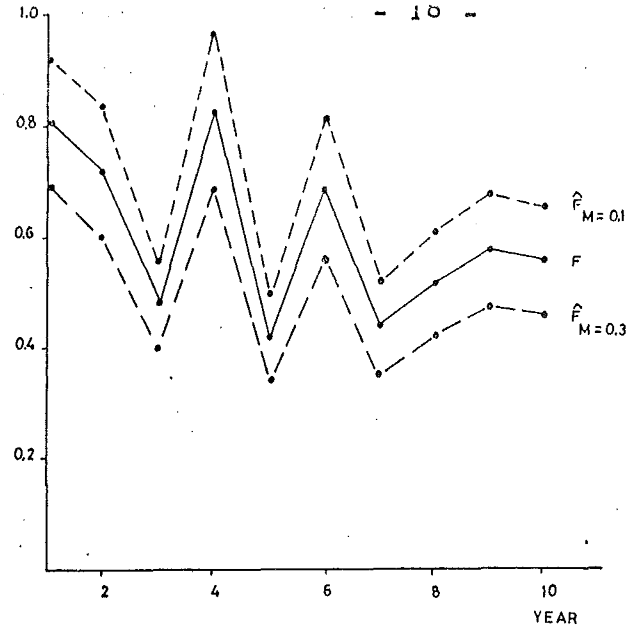

Figure 1. Estimated F-values assuming M= 0.1 and M= 0.3 in VPA plotted together with true F-values (M= 0.2)

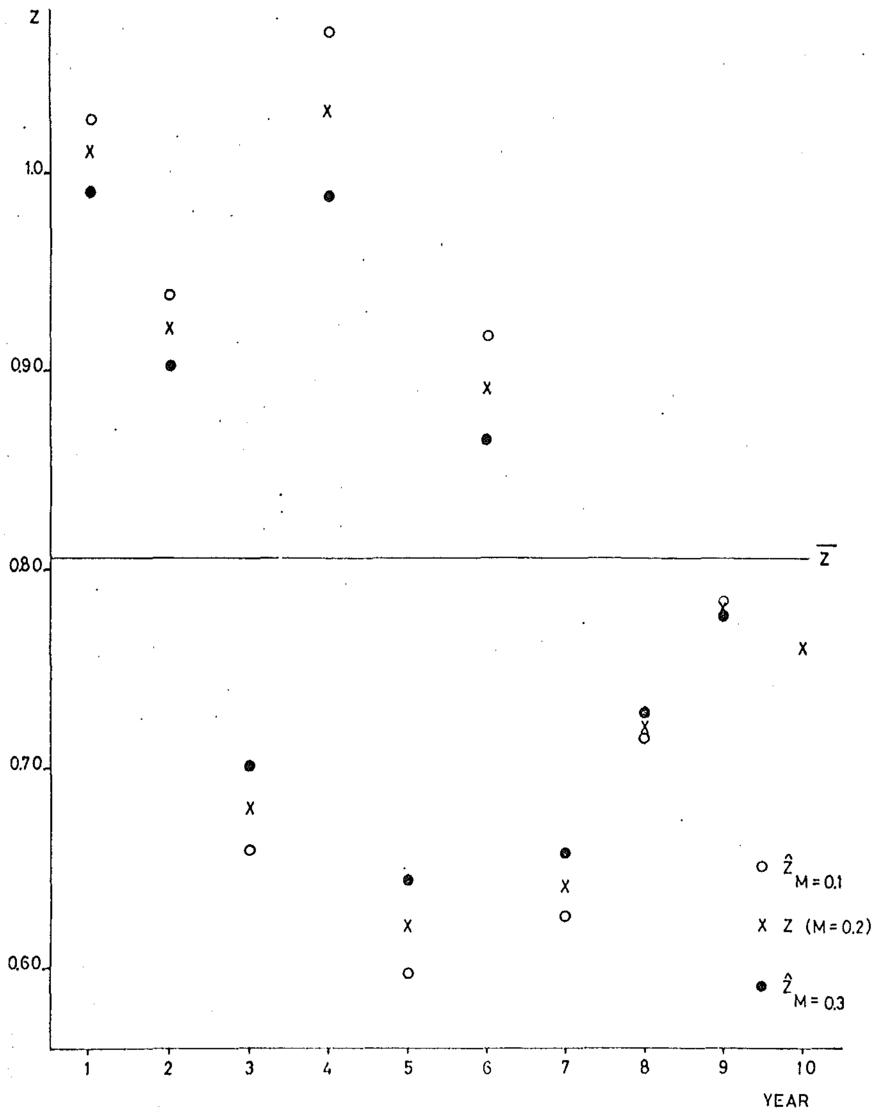

Figure 2. Estimated Z-values assuming M= 0.1 and M= 0.3 plotted together with true Z-values (M= 0.2)

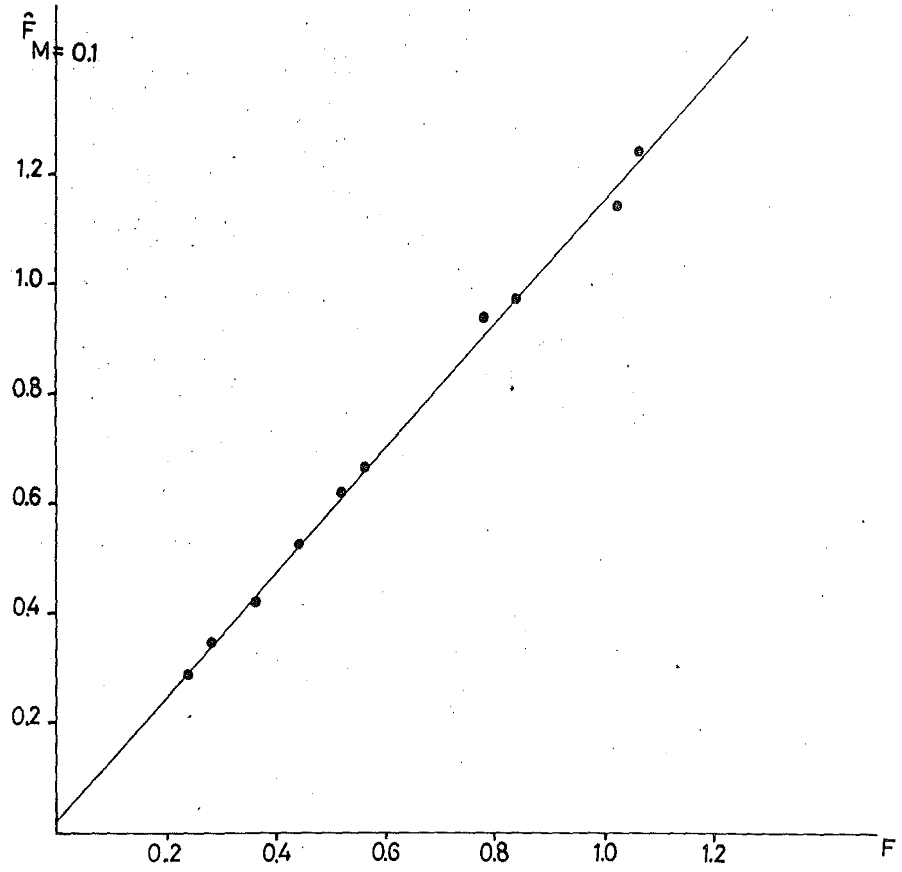

Figure 3. Regression of estimated F-values from VPA assuming M= 0.1 against true F-values (M= 0.2)

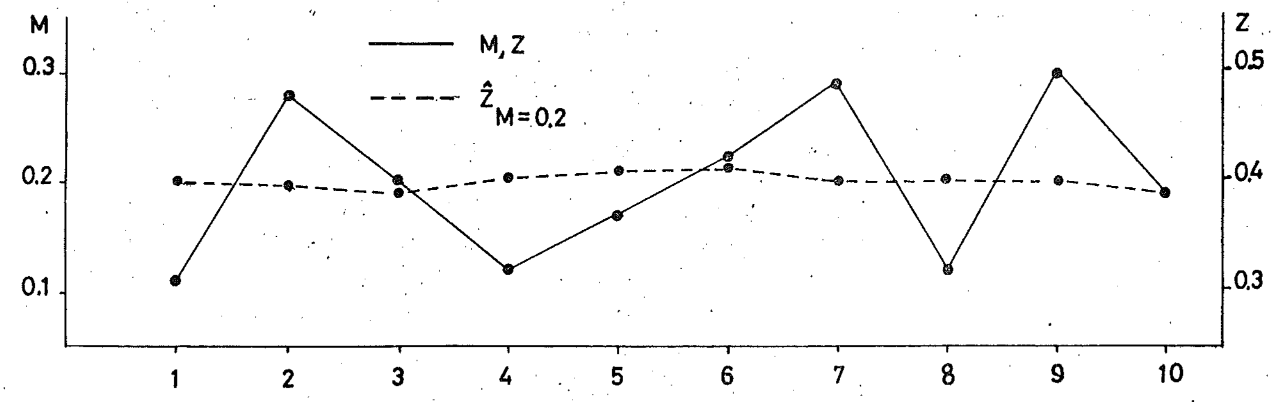

Figure 4a. Estimated total mortality $\hat{Z}$ assuming constant M= 0.2 in VPA plotted together with true (varying) natural and total mortality. F= 0.2

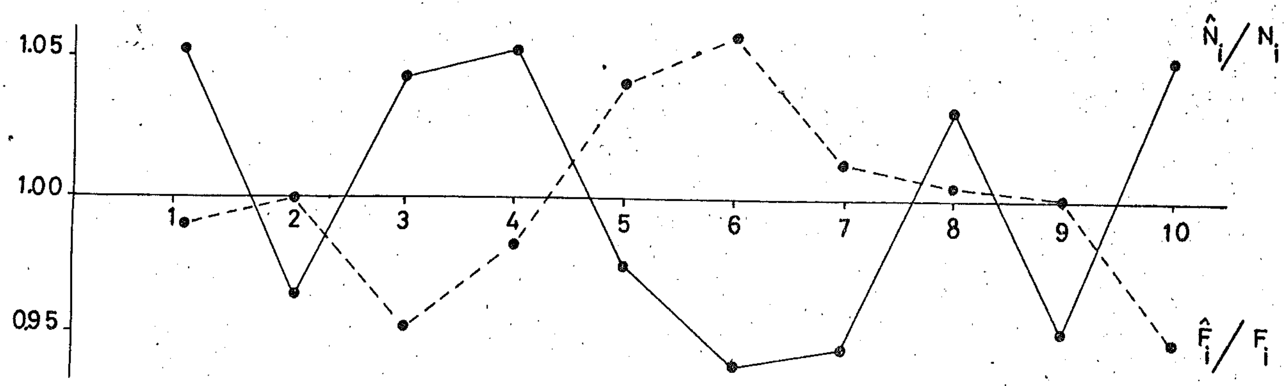

Figure 4b. Relative errors in $\hat{N}_i$ and $\hat{F}_i$. Value of parameters as in Fig. 4a.

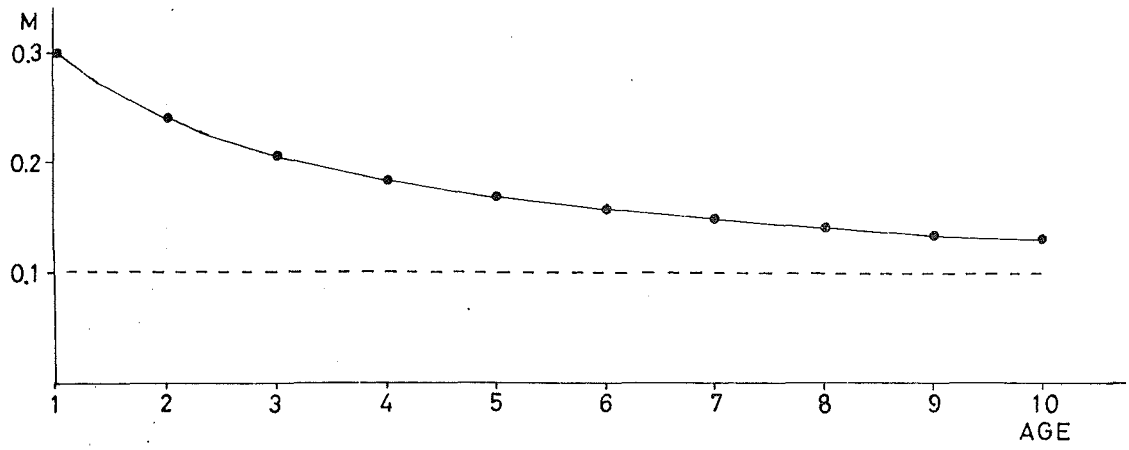

Figure 5a. Natural mortality plotted against age (i) when $M_{i+1} = M_i(1 - (M_i - 0.1))$

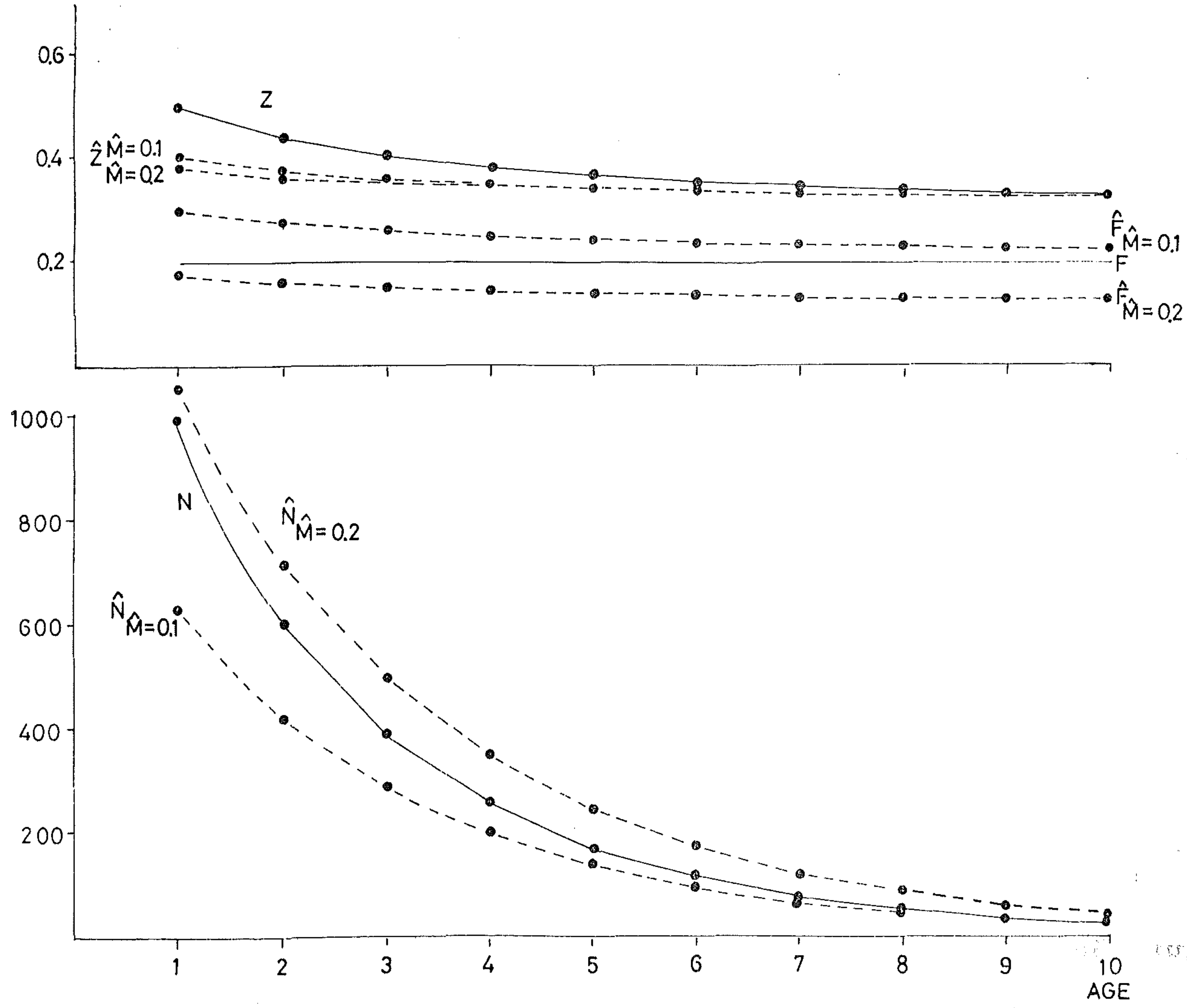

Figure 5b. Estimated Z-values and F-values (upper figure) and N-values (lower figure) from VPA assuming M= 0.1 and M= 0.2 plotted together with true values when M varies with age as in Fig. 5a. F= 0.2

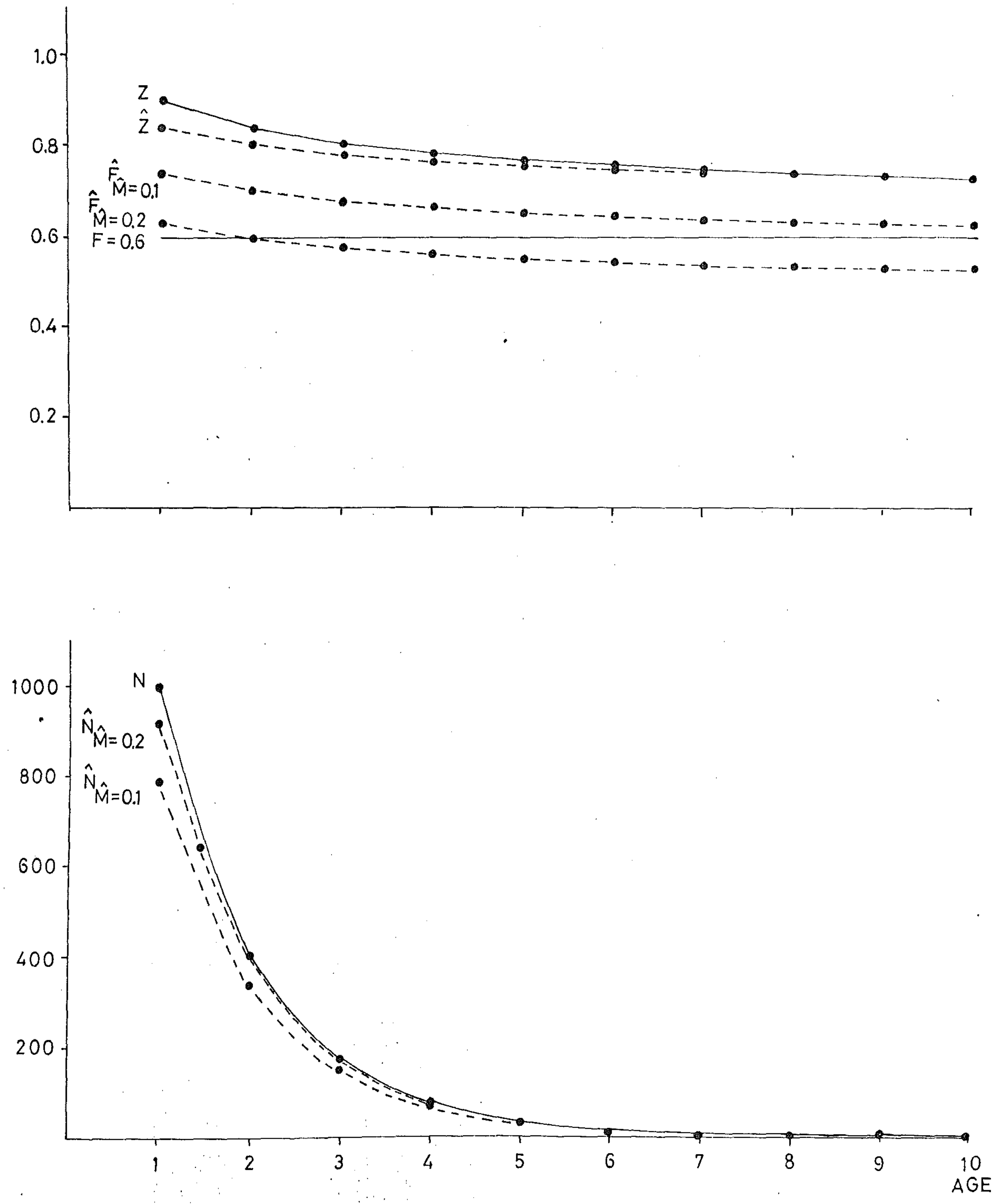

Figure 5c. Estimated Z-values and F-values (upper figure) and N-values (lower figure) from VPA assuming M= 0.1 and M= 0.2 plotted together with true values when M varies with age as in Fig. 5a. F= 0.6

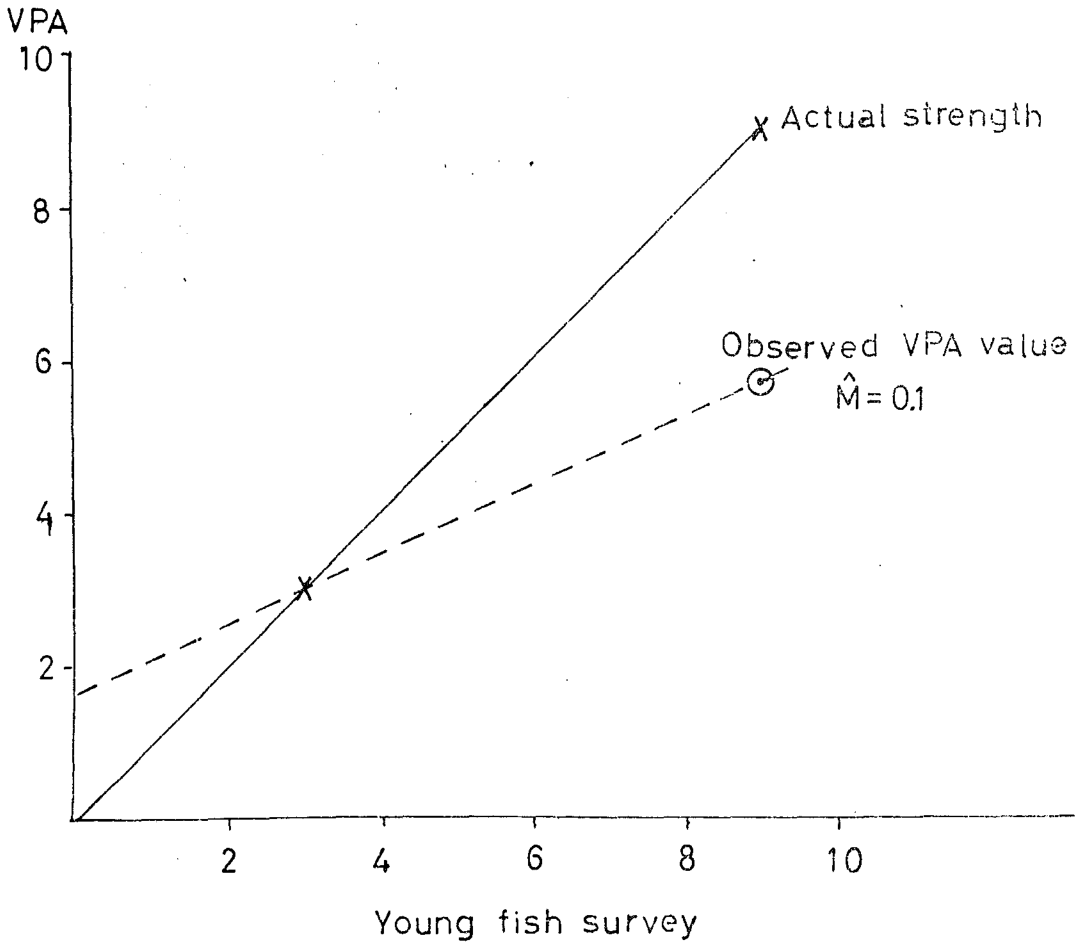

Figure 6. Relation between estimated strength of a yearclass from VPA and young fish trawl surveys when M varies with yearclass strength. For further explanation see text.

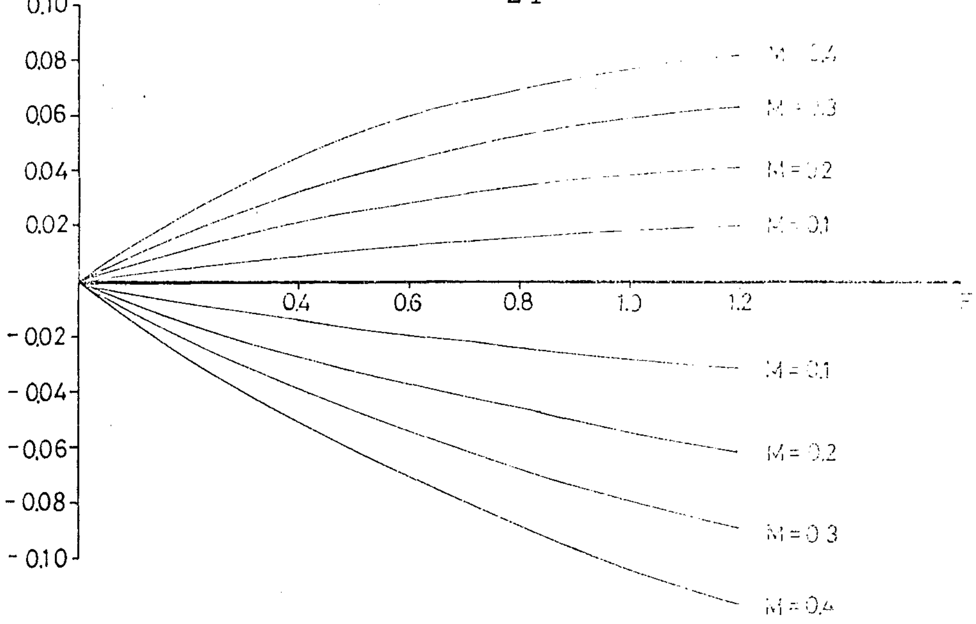

Figure 7. Relative errors in estimated $\hat{N}_{i-1}$ from VPA, caused by uneven seasonal distribution of the fishery, plotted against true annual fishing mortality. $\hat{N}_i$ is assumed to be equal to the true N_i. Positive errors: All catch is taken in the first quarter of the year. Negative errors: All catch is taken in the last quarter of the year.

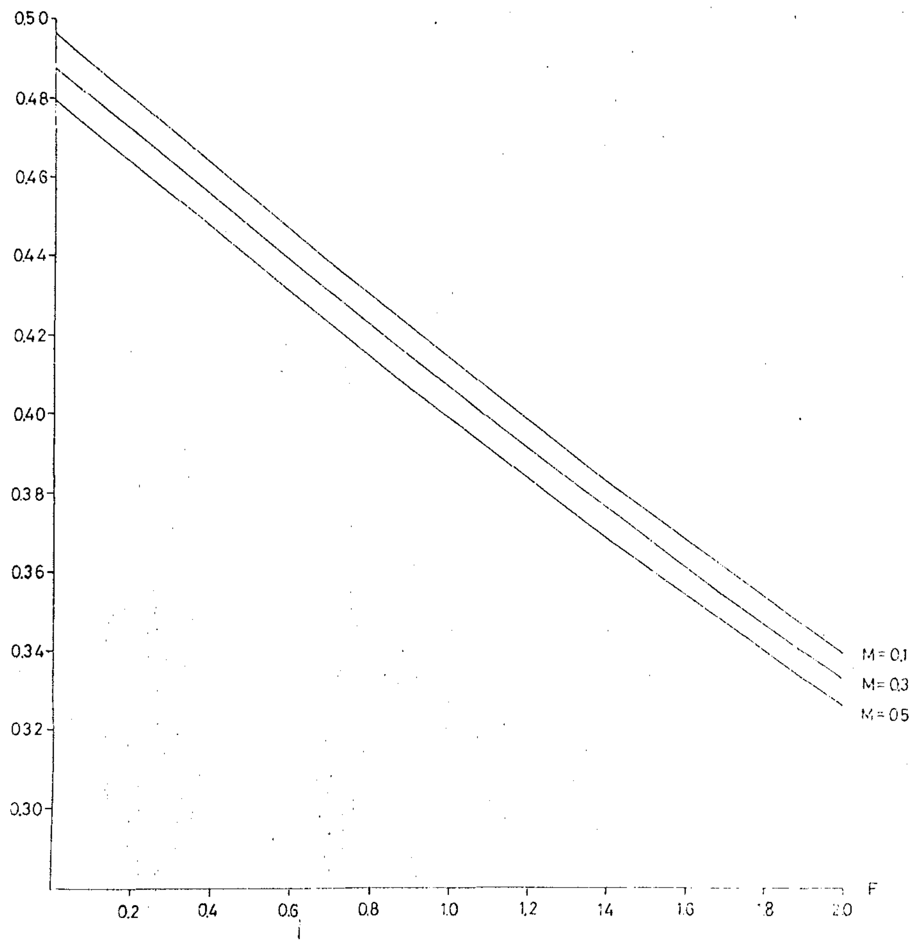

Figure 8. k in the relationship $N_i = C_i e^{km} + N_{i+1} e^M$ plotted against F_i for M= 0.1, 0.3 and 0.5.

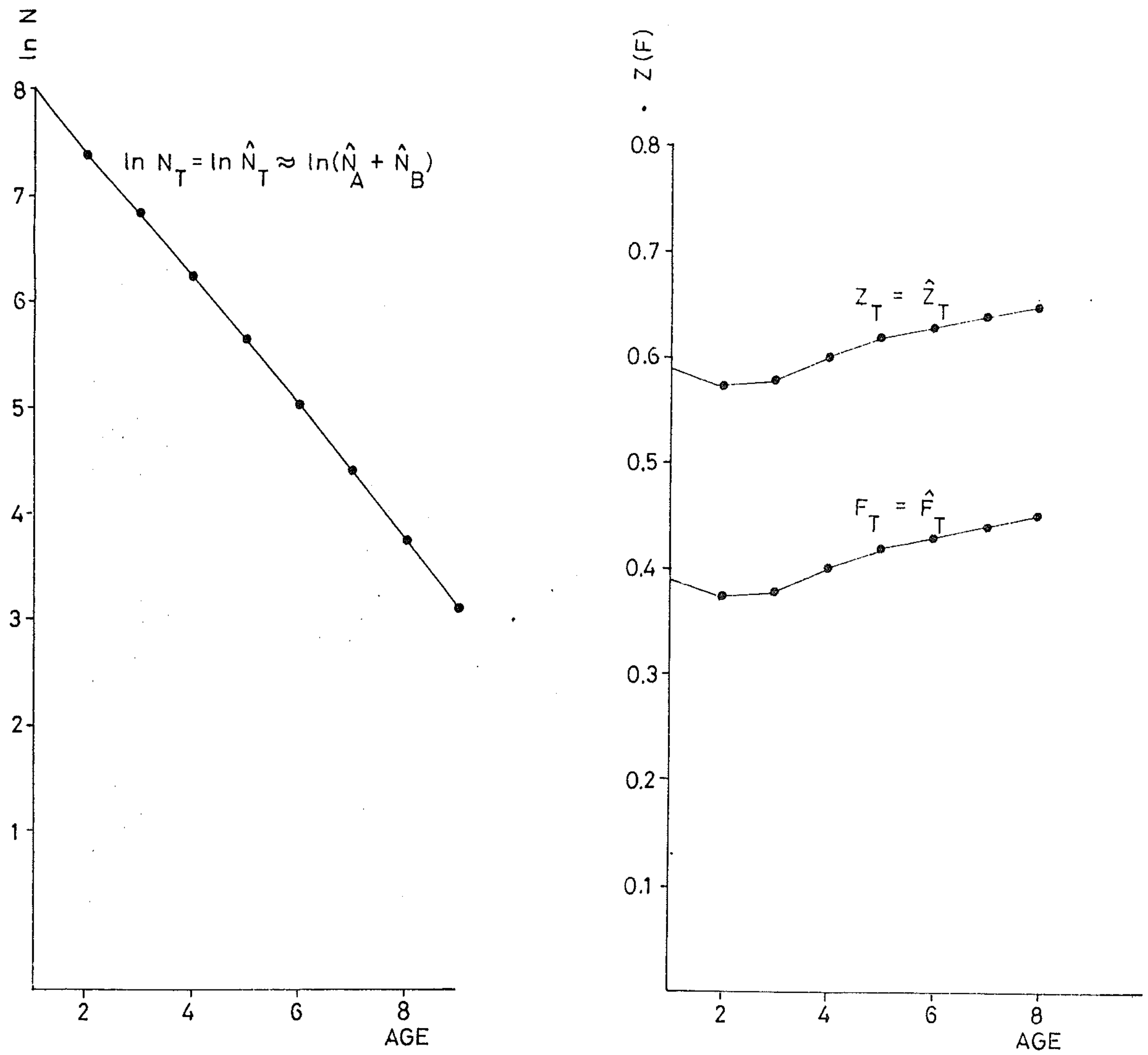

Figure 9a. Logarithm of number of fish (ln N_T), total mortality (Z_T) and fishing mortality (F_T) at different ages for areas A and B combined. For further explanation see section 6.

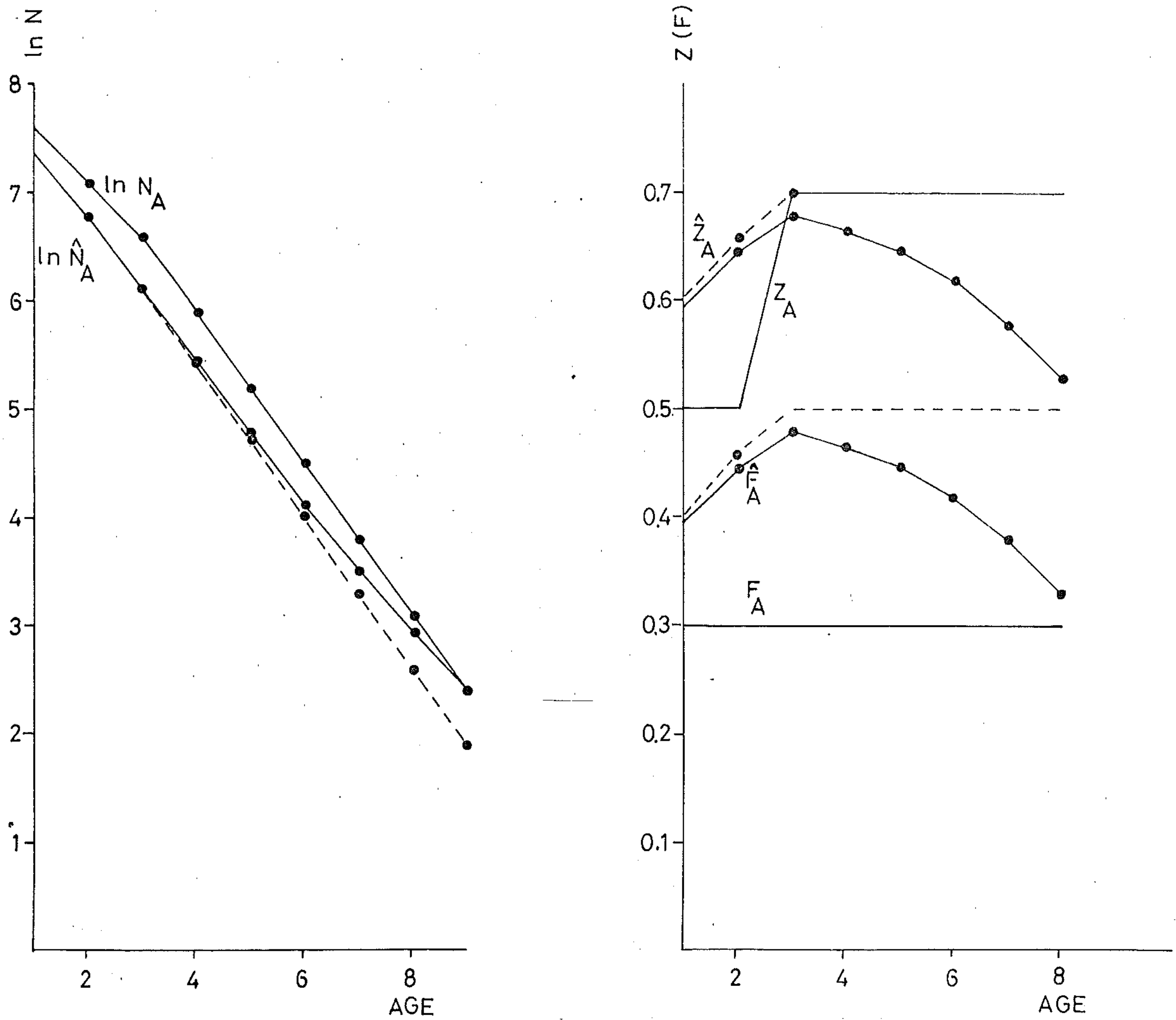

Figure 9b. Logarithm of estimated number of fish (ln $\hat{N}_A$), estimated total mortality ($\hat{Z}_A$) and estimated fishing mortality ($\hat{F}_A$) at different ages from VPA for area A (Whole line: $\hat{N}_{A,9}$ assumed equal to $N_{A,9}$. Broken line: $\hat{Z}_{A,8}$ assumed equal to $Z_{A,8}$) together with true values. For further explanation see section 6.

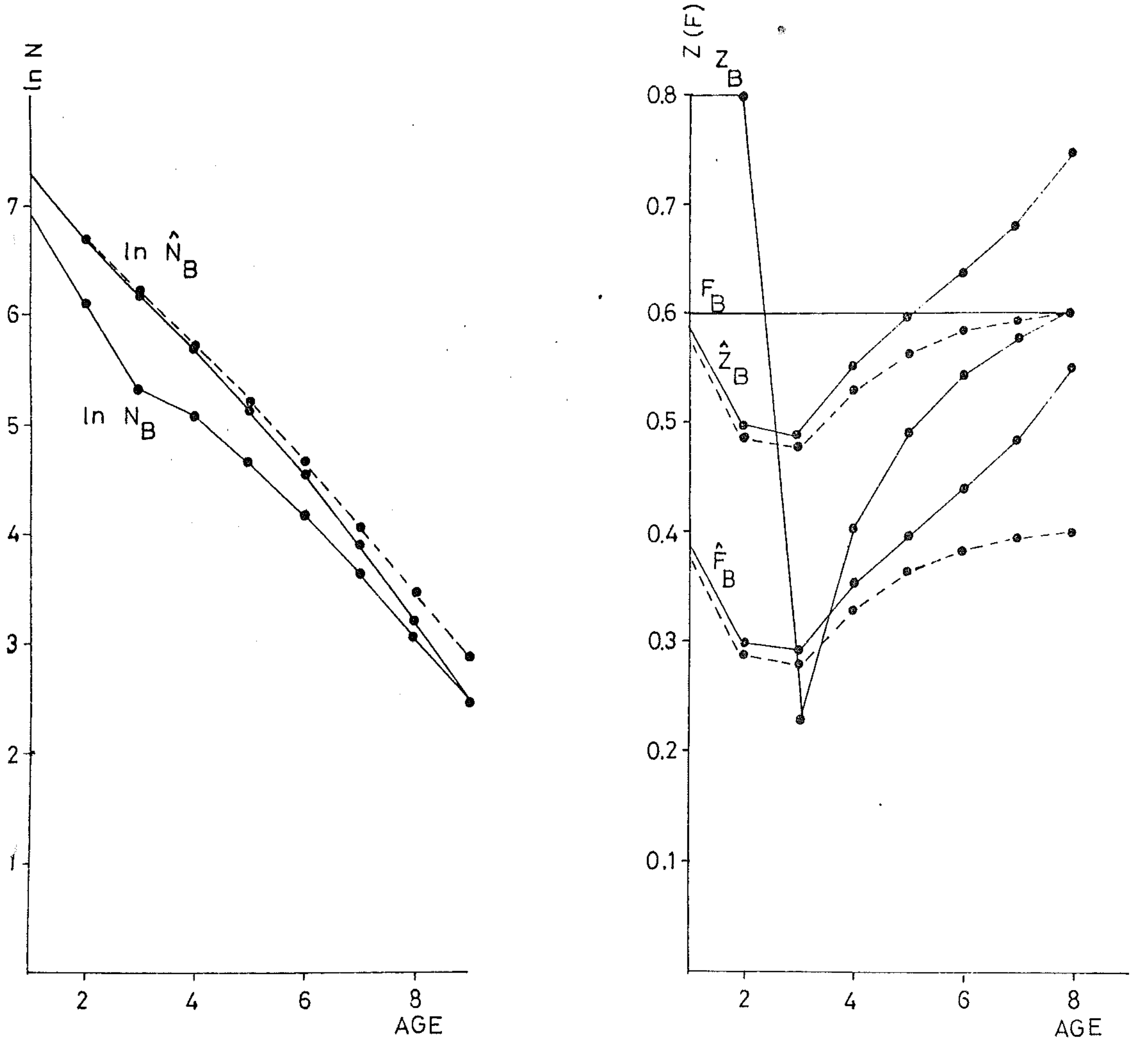

Figure 9c. Logarithm of estimated number of fish (ln $\hat{N}_B$), estimated total mortality ($\hat{Z}_B$) and estimated fishing mortality ($\hat{F}_B$) at different ages from VPA for area B (Whole line: $\hat{N}_{B,9}$ assumed equal to $N_{B,9}$. Brocken line: $\hat{Z}_{B,8}$ assumed equal to $Z_{B,8}$) together with true values. For further explanation see section 6.