INTERNATIONAL COUNCIL FOR THE
EXPLORATION OF THE SEA

VIRTUAL POPULATION ANALYSIS AND MIGRATION A THEORETICAL TREATMENT

by

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INTERNATIONAL COUNCIL FOR THE   Demersal Fish (Northern)Committee
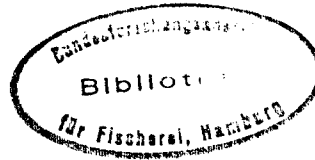EXPLORATION OF THE SEA   Demersal Fish (S)
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VIRTUAL POPULATION ANALYSIS AND MIGRATION
A THEORETICAL TREATMENT
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Introduction

One of the basic assumptions underlying the Virtual Population
Analysis (VPA)is the concept of the unit stock; that means, there
should be no increase or decrease of the population due to migra-
tion. In cases where it is obvious that migration takes place be-
tween populations, questions arise about the reliability of the
recruitment and fishing mortality estimates from the VPA and the
interpretation of the results. This has been the case for instance
with the assessment of the Saithe (Gadus virens L.) (Anon., 1974).
An extensive literature is available on the long distance migra-
tion of this species (Anon., 1965; Jakobsen, 1974; Joensen, 1961;
Jones and Jonsson, 1971; Olsen, 1959 a,b, 1961). Although in view
of the migratory movements of the Saithe the ICES statistical
areas cannot be considered to be completely functional areas in
respect of the unit stock concept, assessments have been made
resulting in recruitmentestimates for each area (Anon., 1974).
Curiously, when these figures are added, one gets almost the same
result as from the VPA applied to the total catches (Anon., 1974).

In the following an attempt has been made, by means of a mathema-
tical model to make this summability plausible and to get an answer
to the question to what extent the estimates of recruitment and
fishing mortality in the separate areas can be biased,

From the continuous to the discrete

First we derive the equations of the VPA by going out of the
following continuous system:

$$\frac{dN}{dt} = - (F+M)N$$

(1)

$$\frac{dC}{dt} = FN$$

N (t) is as usual the population of one yearclass; C (t) is the catch and t is the time.
Solving (1) with initial conditions : N = N (i) and C (i) = 0, substituting (i + 1) for t (F may depend on (i) in this form) and finally replacing C (i + 1) by C (i) to get consistency with the usual notation, we have:

(2) $\qquad N(i+1) = N(i)\ e^{-\ (F(i)+M)}$

(3) $\qquad C(i) = \dfrac{F(i)}{F(i)+M}\ N(i)\ (\ 1 - e^{-(F(i)\ +\ M)})$.

Beverton and Holt(1957, page 142) make use of a continuous system to calculate the yield in weight for two areas taking migration between the areas into account.
We can use their system for our present purpose and add two equations for the catch in each area. Thus we have the system:

$$\frac{dN_1}{dt} = - (F_1 + M_1 + T_1)\ N_1 + T_2 N_2$$

$$\frac{dN_2}{dt} = - (F_2 + M_2 + T_2)\ N_2 + T_1 N_1$$

(4)

$$\frac{dC_1}{dt} = F_1 N_1$$

$$\frac{dC_2}{dt} = F_2 N_2$$

The indices 1 and 2 stand for the two areas.
T1 (T2) is the transportcoefficient for the migration from area 1 (2) to area 2 (1). These parameters are just as F and M positive constants.
We proceed in the same manner as we did with system (1).
Fist solving (4) with initial conditions $N_j = N_j$ (i) and C_j (i) =o (where j = 1,2), then substituting (i + 1) for t and replacing C_j (i + 1) by C_j (i), we arrive at:

(5) $\qquad N_1\ (i + 1) = X_1 e^{-\ a\ +\ b} + X_2 e^{-\ a\ -\ b}$

(6) $\qquad N_2\ (i + 1) = X_3 e^{-\ a\ +\ b} + X_4 e^{-\ a\ -\ b}$

(7) $\qquad C_1 (i) = F_1 (\dfrac{X_1}{-a+b}\ e^{-\ a+b} + \dfrac{X_2}{-a-b}\ e^{-a-b} + C_1)$

(8) $\qquad C_2 (i) = F_2 (\dfrac{X_3}{-a+b}\ e^{-\ a+b} + \dfrac{X_4}{-a-b}\ e^{-a-b} + C_2)$,

where we have used the following abbreviations:

$$X_1 = (N_1 (i) (-c + b) + N_2 (i) T_2) / (2b)$$

$$X_2 = (N_1 (i) (c + b) - N_2 (i) T_2) / (2b)$$

$$X_3 = (N_2 (i) (c + b) + N_1 (i) T_1) / (2b)$$

$$X_4 = (N_2 (i) (-c + b) - N_1 (i) T_1) / (2b)$$

$$a = (k_1 + k_2) / 2$$

$$c = (k_1 - k_2) / 2$$

$$b = (c^2 + T_1 T_2)^{1/2}$$

$$k_1 = F_1 (i) + M_1 + T_1$$

$$k_2 = F_2 (i) + M_2 + T_2$$

$$C_1 = (N_1(i) k_2 + N_2 (i) T_2) / (k_1 k_2 - T_1 T_2)$$

$$C_2 = (N_2(i) k_1 + N_1 (i) T_1) / (k_1 k_2 - T_1 T_2)$$

The a, b, c, k_1 and k_2 are used throughout this paper to get minimal notations. Note relations between them like:

$$a + c = k_1; \quad a - c = k_2; \quad (- a + b) (- a - b) = k_1 k_2 - T_1 T_2;$$

$$X_3 = X_1 (c + b) / T_2 \quad \text{and} \quad X_4 = X_2 (c - b) / T_2.$$

A simultaneous VPA for two areas

In simplifying the application of equation (2) and (3) to catch-numbers, the N (i)- terms are eliminated from (2) and (3) to get a third equation in which F is the only unknown.
This root can be obtained by means of an iterative procedure. (Pope, 1972). The same can be done with formulas (5), (6), (7) and (8). The Nj (i) terms are linearly represented in X_1 until X_4, so they can also be eliminated in order to get two new relations in which F_1 and F_2 are the only unknowns.
From (7) and (8) we get the prescription to calculate Nj (i), when Fj (i) is known. Omitting the (i) we have:

$$(9) \qquad N_1 = (F_2 C_1 (A e^{- a + b} + B e^{- a - b} - k_1) + F_1 T_2 C_2 H)/(F_1 F_2 G)$$

$$(10) \qquad N_2 = (F_1 C_2 (D e^{- a + b} + E e^{- a - b} - k_2) + F_2 T_1 C_1 H)/(F_1 F_2 G).$$

The two relations, which are to be solved for Fj (i), are:

(11) F_2C_1 (Be^{-a+b} + Ae^{-a-b} $-k_1$e^{-2a}) + $F_1T_2C_2$J + $F_1F_2N_1$ (i+1) G = 0

(12) F_1C_2 (Ee^{-a+b} + De^{-a-b} $-k_2$e^{-2a}) + $F_2T_1C_1$J + $F_1F_2N_2$ (i+1) G = 0,

where for convenience we used the following abbreviations:

A = (k_1 (c + b) + T_1T_2)/(2b)

B = (k_1 (-c+b) - T_1T_2)/(2b)

D = (k_2 (-c+b) + T_1T_2)/(2b)

E = (k_2 (c + b) - T_1T_2)/(2b)

G = e^{-a+b} + e^{-a-b} - e^{-2a} -1

H = ((- a-b)e^{-a+b} -(-a+b) e^{-a-b})/(2b) + 1

J = ((- a-b)e^{-a-b} -(-a+b) e^{-a+b})/(2b) + e^{-2a}

Equations (11) and (12) are analogous to:

(13)   C (F + M) e$^{-(F+M)}$ + FN (i + 1) (e$^{-(F + M)}$ -1) = 0,

Which is the central relation in the standard VPA.
The latter has a parabola - like shape with two roots:
F = -M and another positive one, which can't be found expli-
citly (otherwise iteration wouldn't be necessary).
Let's call (11) f 1 = 0 and (12) f 2 = 0.
Both f 1 and f 2 are functions of F 1 and F 2 and may be visuali-
zed as three dimensional surfaces. In vertical cross-section
parallel to one of the F - axes they have the same parabola-
like shape as (13). When - a + b = 0, then A = k_1 and D = k_2
and both f 1 and f 2 vanish. The same happens for - a - b = 0.
Consequently k_1k_2 - T_1T_2 = 0 is a solution (one should say con-
tains infinitely many solutions) of f 1 = f 2 = 0. This func-
tion determines an orthogonal hyperbola with asymptotes in F_1 =
- (M_1 + T_1) and F_2 = - (M_2 + T_2).
Just as with (13), there are other solutions of (11) and (12)
which can't be obtained analytically.
These solutions seem to be hyperbolas too, one for f 1 = 0 and
one for f 2 = 0. They intersect at two points: the origin and
the one and only positive combination, the roots we were looking
for. Illustrative sketches can be found in figures 5 and 6.
The iteration of (11) and (12) can be done with any suitable
numerical procedure. For an example, see appendix 1.

The results of some numerical experiments

When trying to evaluate how the estimates resulting from the standard VPA are influenced by migration it appears to be almost impossible to handle the problems analytically. Therefore it is more suitable to substitute numerical values for the parameters and see what happens, although a big problem arises when proceeding in this way. The number of combinations one can make up from a few values for several parameters increases so fast with the number of parameters that one is really limited in such an approach and therefore one can hardly expect to get any structural insight. Fortunately, however, in the present case an important feature of the model was revealed after a few simulations.

We created catches according to equations (5), (6), (7) and (8) with the following parameter values:

Series 1:

$N_1 (0) = 100$ $N_2 (0) = 10$

$F_1 (0) = .07$ $F_2 (0) = .1$

$F_1 (1) = .27$ $F_2 (1) = .4$

$F_1 (2) = .33$ $F_2 (2) = .5$

$F_1 (3,...,9) = .4$ $F_2 (3,...,9) = .6$

$M_1 = M_2 = .2$

T_1 and T_2 were chosen in 36 combinations each between 0 and .2, ascending with steps of .04 (constant during the lifespan; of course one can make T (i)-dependent).

Series 2:

The same parameter values except that $N_1(0) = 50$ and $N_2 (0) = 100$. To the catches of both areas, separately and combined, we applied the normal VPA with terminal fishing mortalities:
.4 for area one, .6 for area two and .5 for the added catches. First we refer to sketches of two selected runs (figures 1 and 2). Run I was chosen from series 1 with $T_1 = .08$ and $T_2 = .04$. Run II was chosen from series 2 with $T_1 = .04$ and $T_2 = .12$. It would be possible to give a complete list of the deviations of the estimated values resulting from the VPA from the input fishing mortalities and population numbers, but of particular interest is the deviation between the recruitments and the recruitment estimates. It turned out that the difference between $N_1(0)$ and the estimated recruitment in area 1 (R_1) was equal to the difference between R_2 and $N_2(0)$, thus $R_1 + R_2 = N_1 (0) + N_2 (0)$.

The estimated recruitment from the total catches (R) was also equal to N_1 (0) + N_2 (0). For example for run I we found: R_1 = 78.69; R_2 = 31.29 (R_1 + R2 = 109,98); R= 109,73, and for run II we found: R_1 = 69.11; R_2 = 80.89 (R1 + R2 = 150.00); R = 149.61.
The deviations of the recruitment estimates of series 1 and 2, given as   are drawn as functions of

$$\frac{R_1 - N_1 (0)}{N_1 (0)} \times 100\%$$

T_1 and T_2 in figures 7 and 8. The isopleths seemed to be straight lines and are drawn without any advanced interpolation technique. We did many experiments with different parameter values and found the same results with one exception. If one takes $M_1 \neq M_2$, then in general the summability-results do not hold. The problem then becomes how to choose the natural mortality to be used in the VPA. Certainly three natural mortalities (two for the areas and one for the total) can be found which give the same summability - results, but a prescription how to choose these fails.

There is no general rule to be given for the deviations of the fishing mortality estimates from the input fishing mortalities (see figures 3 and 4). The deviations depend completely on the parameters chosen. In figure 3 one sees that the deviations in the F_2 become so large that it might have been better to choose $F_2(t)$ lower.

We can draw the following main conclusions.

1. The deviations in recruitment estimates and in fishing mortality estimates, caused by migration, depend largely on the direction and size of the migratory movements. No general rule can be given.
2. In cases where the recruitments in neighbouring areas differ more than a factor 5, the lower recruitment will always be overestimated and the higher recruitment will be underestimated with any migration pattern. That means, when a relatively low and a high recruitment estimate are derived from the VPA for two neighbouring areas, the low one can be expected to be even lower and the high one higher.
3. The summability of recruitment estimates observed in the results from the VPA for different Saithe stocks (Anon., 1974) is exemplified by numerical simulations with this simple model. The results suggest that the summability itself does not say anything about the reliability of the recruitment estimates for the areas separately, but the total recruitment is likely to be hardly biased, when only the right natural mortality has been applied. This is automatically the case when this mortality has the same value throughout the area.

The convergence of the simultaneous VPA

In order to act as a useful analysis in fisheries research, the simultaneous VPA should converge to the real F-values for different choices of terminal fishing mortalities. To check this feature, we applied the simultaneous VPA to the catches of run I.

/the

In figures 9,10,11 and 12, we give the fishing mortalities coming
out of/simultaneous VPA for different F(t)- combinations.
(Of course: $F_1(t)$ = .4 and $F_2(t)$ =.6 is the right combination).
The manner in which $F_2(i)$ converges, depends not only on $F_2(t)$ but
also on $F_1(t)$: fig. 9, 10 and 11. On the contrary: the manner in which
$F_1(i)$ converges seems hardly to be affected by the choice of $F_2(t)$:
fig. 12. The deviations in both recruitments (not given here)
roughly cancel and don't often exceed 5 population units.

Discussion.

In the numerical experiments we didn't apply migrationcoefficients
greater than the natural mortality. The philosophy behind this is the
consideration that stocks mixing to an even larger extent should not
be considered as unit stocks at all.

Olsen (1959) reports that 3- and 4-year old Saithe seem to be quite
stationary. However the part of the older population that migrates   -
from one stock to another can exceed a value of .2 in terms of/transport /a
coefficient. From figures 7 and 8 it is obvious that even a comparati-
vely small overall migration in one direction may result in a signi-
ficant bias on the recruitmentestimates, especially when the sizes
of the two populations are rather different. A difference between
the fishing mortalities may enlarge this bias or reduce it. Thus,
under such circumstances it might be advisable not to put to much
weight on the individual stock assessments for management purposes,
but base conclusions on the VPA of combined catch data instead. As an
alternative, estimation of the migration parameter values would lead
to increased accuracy of the information on the individual stocks,
because then the simultaneous VPA might be applied.
In practice, the estimation of T= T(i) is as problematic as is the
estimation of M. A good starting point might be the model presented
by Jones (1959) since the migrationcoefficients are related to diffu-
sion processes (Beverton and Holt 1957, page 139).

Some prospects.

The success of the VPA is based on two features: the possibility to
eliminate N(i) and the convergence to the right values of F and N
for different terminal fishing mortalities.
However, without elimination one simply has to iterate two functions
of two variables or four functions of four variables in the simulta-
neous VPA, so the linearity of N is not crucial to the applicability
of the VPA. The convergence for different terminal F's is conserved
in the simultaneous VPA. Since Pope (1972) proved this feature by
means of the formula:

$$r(N(i)) = e^{-F(i)} \cdot r(N(i+1)) \quad ,$$

where r is the proportional error, it seems to be characteristic for
all systems where the fishing mortality is the dominant parameter.

When writing down a system like (4) for several species, specifying trophical interactions between different yearclasses, the system will be essentially nonlinear, so that an analytical solution can not be obtained. In this case it should be possible to construct an inverse numerical procedure that back-calculates population sizes with the same converging chracteristics.
Whether this statement is true, especially in the light of the model of Andersen, Lassen and Ursin (1973) has yet to be studied.

Summary.

The Virtual Population Analysis is generalized to an analysis for two areas, taking into account migration between the areas. The resulting equations are studied.
Some numerical experiments are carried out to see what can be effect of ignoring migration to the original values of populationsize and fishing mortality.

References.

1. Andersen, K.P., Lassen, H. and Ursin, E. 1973. A Multispecies Extension to the Beverton & Holt Assessment Model, with an Account of Primary Production. ICES C.M. 1973/H:20.

2. Anonymus, 1965. ICES, Cooperative Research Report 6.

3. Anonymus, 1974. Report of the Saithe (Coalfish) Working Group. ICES, C.M. 1974/F:2, Demersal Fish (Northern) Comm.

4. Beverton, R.J.H. and Holt, S.J., 1957. On the dynamics of exploited fish populations. London, 19, page 136-144.

5. Jakobsen, T., 1974. Observations on the Spawning Grounds of the North Sea and Norway Coast Stocks of Saithe. ICES, C.M. 1974/F:44.

6. Joensen, J.S., 1961. Coalfish (Gadus virens L.) Investigations at the Faroes. ICES, C.M. 1961, Gadoid Fish Comm. No 94.

7. Jones, B.W. and Jonsson, J., 1971. Coalfish Tagging Experiments at Iceland. Rit Fiskideildar. V Bindi-Vol.V, nr.1.

8. Jones, R., 1959. A Method of Analysis of some Tagged Haddock Returns. Journal du Conseil, Vol. 25, nr. 1, page 58-72.

9. Olsen, S., 1959a. Migrations of Coalsfish (Gadus virens L.) from Norway to Faroe Islands and Iceland. ICES, C.M. 1959, Gadoid Fish Committee, nr. 12.

_____, 1959b. Preliminary Results of the Norwegian Coalfish Taggings '54-'58. ICES, C.M. 1959, Gad. Fish Comm., nr. 114.

_____, 1961. An account of the Norwegian Coalfish Investigations with special reference to the Tagging Experiments. ICES, C.M. 1961, Gad. Fish Comm., nr. 125.

10. Pope, J.G., 1972. An Investigation of the Accuracy of Virtual Population Analysis using Cohort Analysis. ICNAF Research Bulletin, nr.9, page 65-74.

11. Stoer, J., 1972. Einführung in die Numerische Mathematik I. (Springer V., Berlijn).

Legend to the figures.

Fig. 1a. Population numbers according to equations (5) and (6) with
the parametervalues of run I.
Fig. 1b. The catches in both areas according to equations (7) and
(8) in the same units but on a different scale.
Fig. 2. The same as fig.1, but with the parametervalues of run II.
Fig. 3. Input fishing mortalities (black dots) and fishing
mortalities resulting from the standard VPA applied to the
catches of run I (open squares). The stars represent the
fishing mortalities resulting from the combined catches.
Fig. 4. The same as fig.3 for run II.

Fig. 5. Solutions of equations (11) and (12) with the following data:
$C_1(i)= 7.57$; $(2(i)=11.78$; $N_1(i+1)=14.19$; $N_2(i+1)=13.19$;
$M_1=M_2=.15$; $T_1=T_2=.10$; Positive solution: $F_1=.4$, $F_2=.6$.

Fig.6. The same as fig.5 with these data:
$C_1(i)=15.04$; $C_2(i)= 24.47$; $N_1(i+1)=54.88$; $N_2(i+1)=32.41$;
$M_1=M_2=.2$; $T_1=.2$; $T_2=0$; Positive solution $F_1=.2$ $F_2=.6$.

Fig.7. The isopleth diagram of $\dfrac{R_1-N_1(0)}{N_1(0)}$ x 100% ($N_1(0)$ input-

recruitment , R_1 estimated recruitment with standard VPA)
according to series 1. The recruitment deviation being
plotted as function of T_1 and T_2.
Fig.8. The same as fig. 7 for series 2.

Fig.9,10, 11 and 12. Fishing mortalities resulting from the simul-
taneous VPA applied to run I, for different terminal F's.
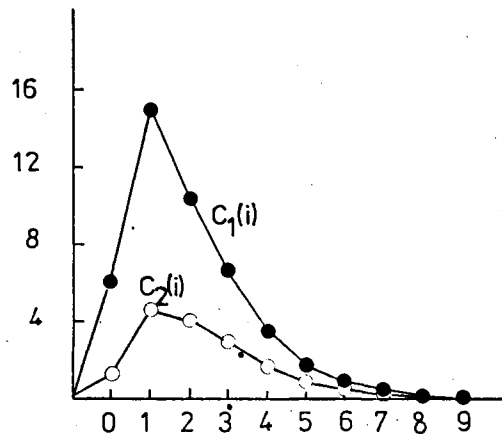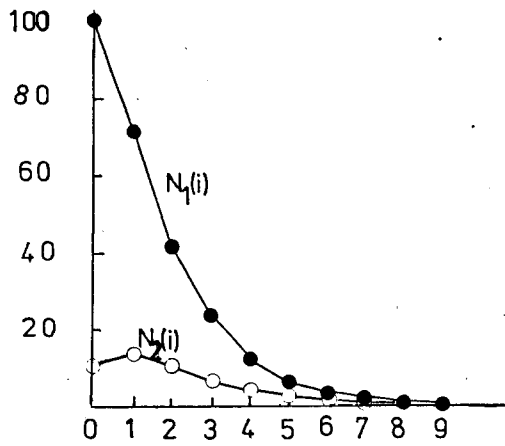
fig.1a,1b
Run I
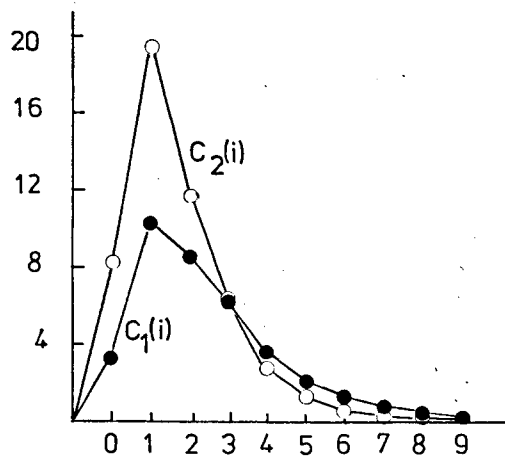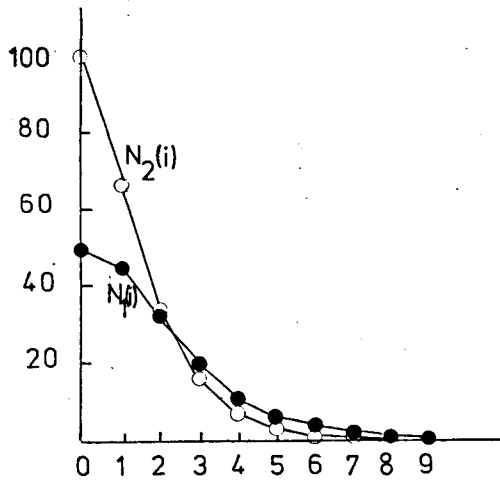
fig.2a,2b
Run II
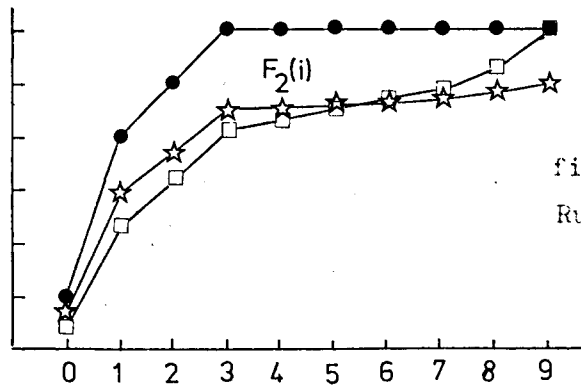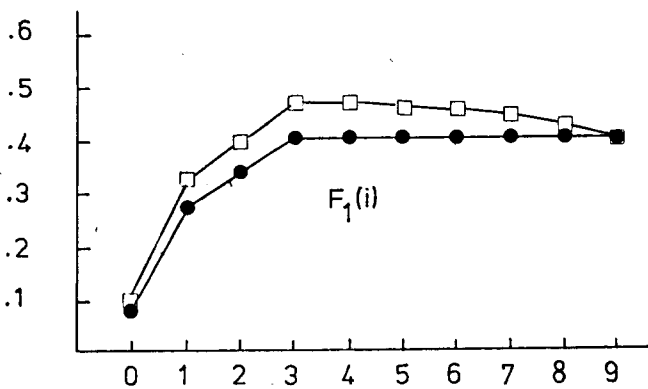
fig.3a,3b
Run I
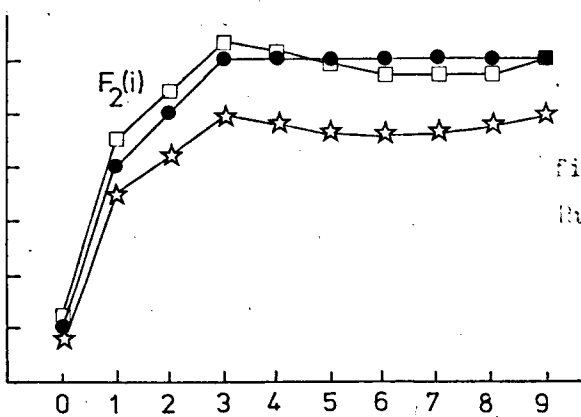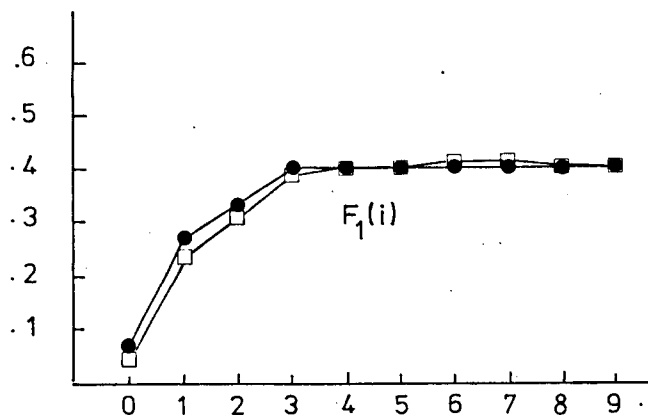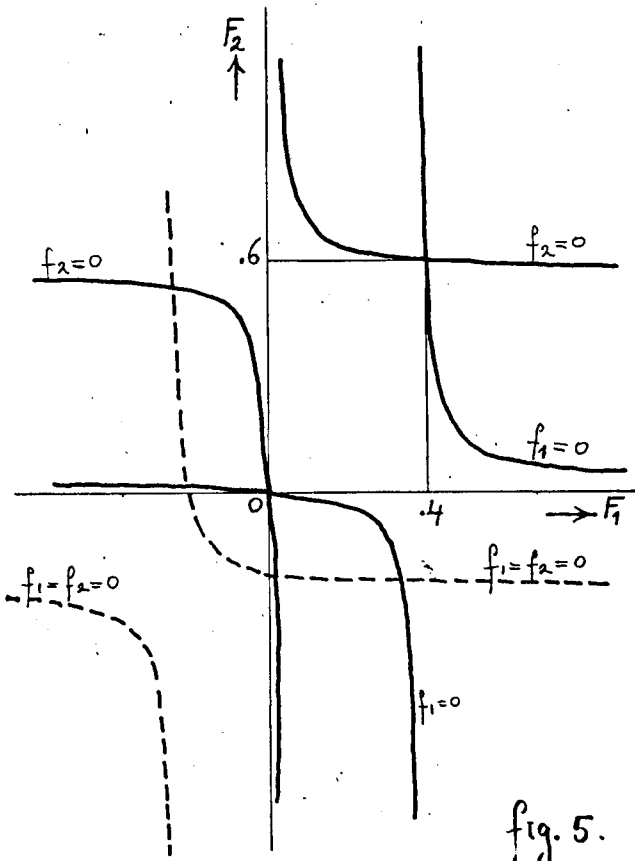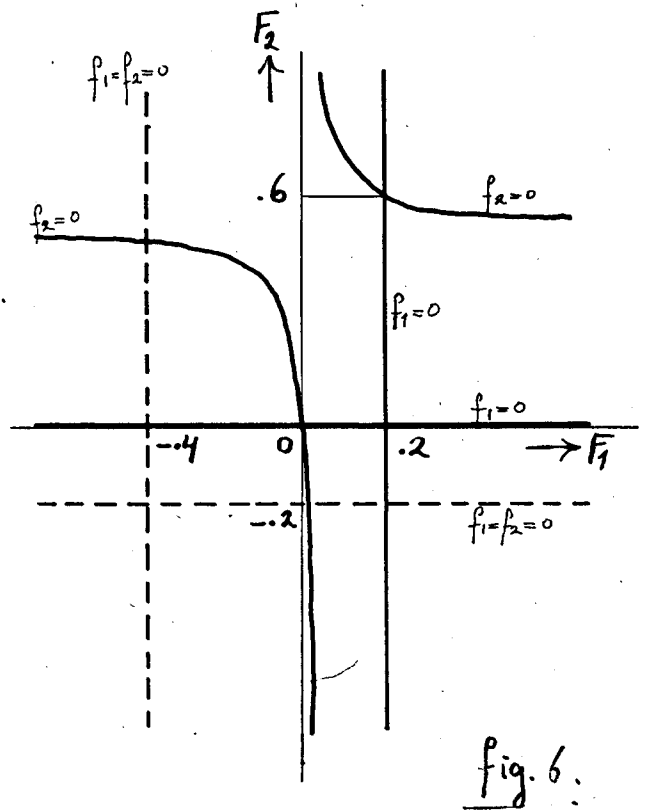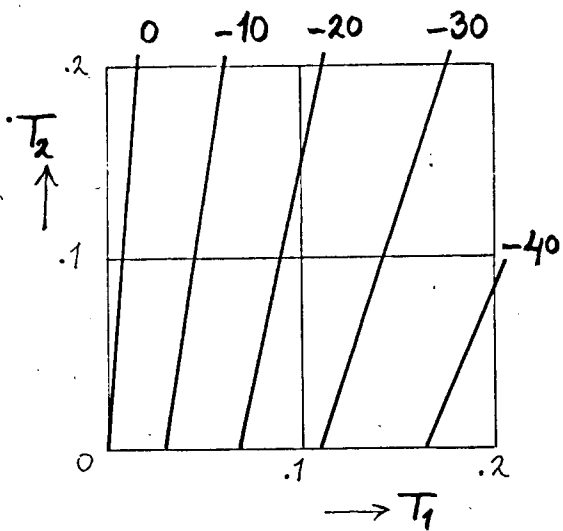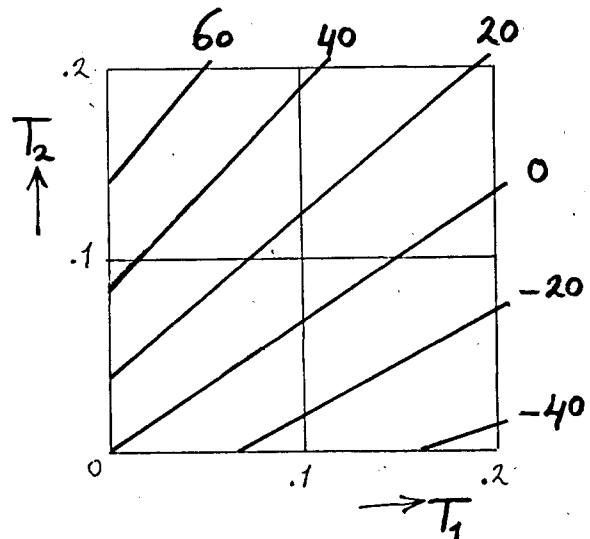
fig.4a,4b
Run II

fig. 5.

fig. 6.

fig. 7.

fig. 8.

Fig. 9 — $F_2(i)$ versus i, with $F_1(t) = .2$

Fig. 10 — $F_2(i)$ versus i, with $F_1(t) = .4$

Fig. 11 — $F_2(i)$ versus i, with $F_1(t) = .6$
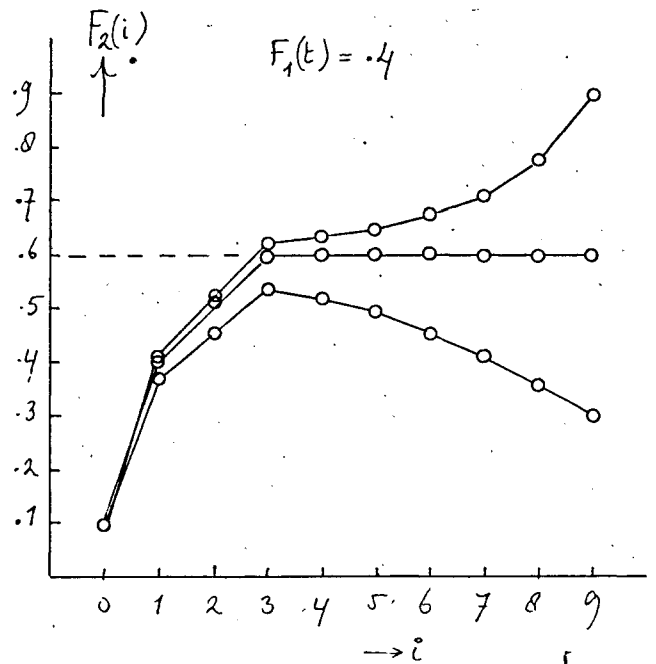
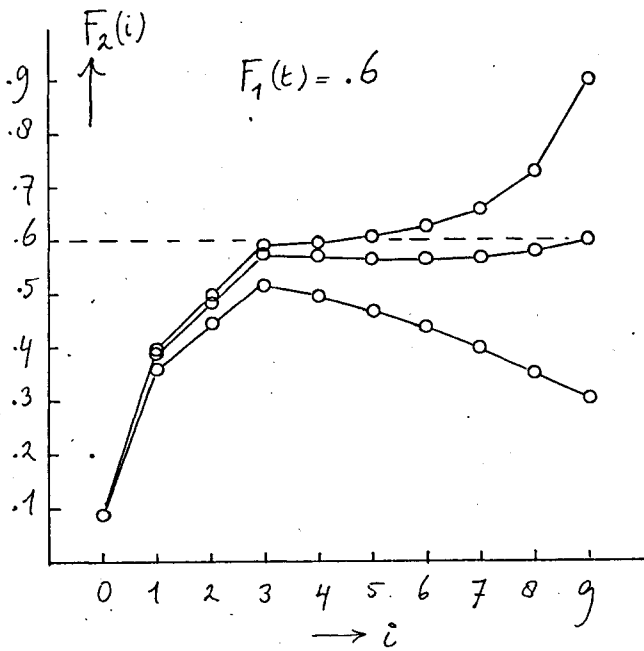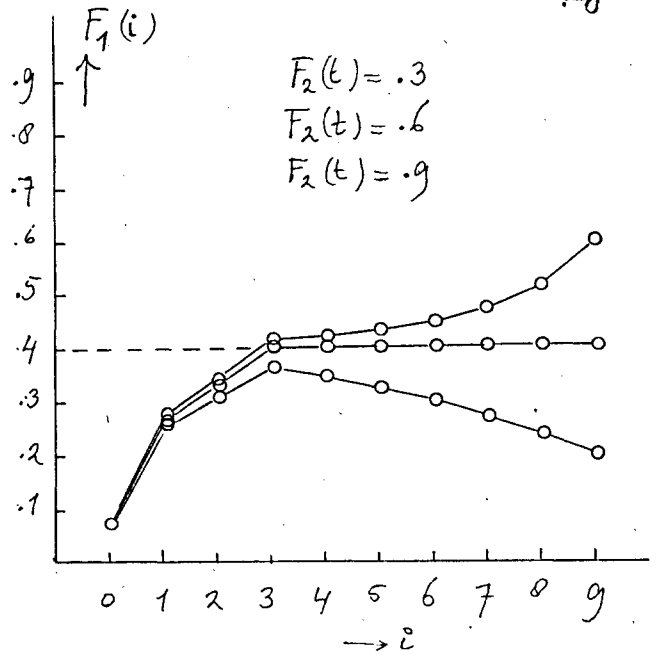Fig. 12 — $F_1(i)$ versus i, with $F_2(t) = .3$, $F_2(t) = .6$, $F_2(t) = .9$

1
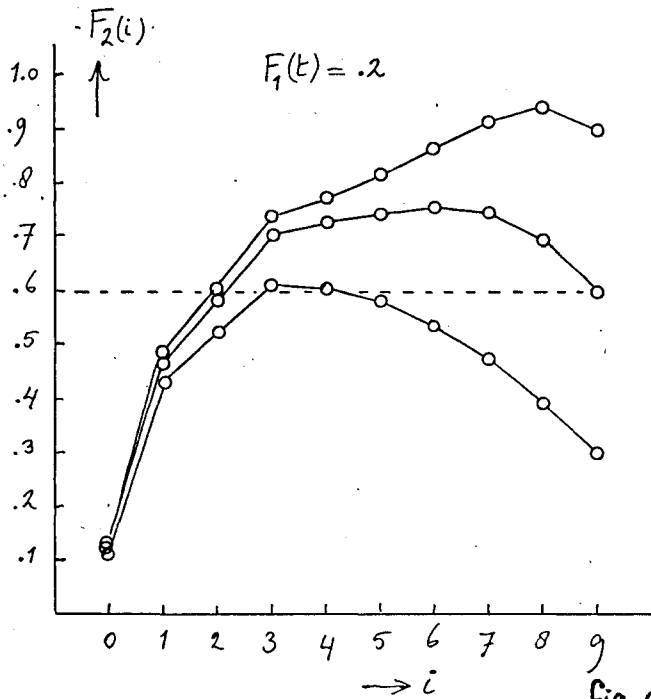
Appendix 1.

The method we used to solve (11) and (12) for $F_1(i)$ and $F_2(i)$, is a generalization to two variables of a method called "regula falsi" (Stoer, 1972).
Using the short notations $f(j,j-1)$ for $f(F_1^j, F_2^{j-1})$ and $f(j)$ for $f(F_1^j, F_2^j)$, we have the algorithm ($j= 0,1,2,\ldots$):

$$F_1^{j+1} = F_1^j - (F_1^{j-1} - F_1^j) (f_2(j,j-1).f_1(j) - f_1(j,j-1).f_2(j))/N$$

$$F_2^{j+1} = F_2^j - (F_2^{j-1} - F_2^j) (f_1(j-1,j).f_2(j) - f_2(j-1,j).f_1(j))/N ,$$

where

$$N= f_1(j-1,j).f_2(j,j-1) - f_1(j,j-1).f_2(j-1,j) +$$

$$+ f_1(j).(f_2(j-1,j) - f_2(j,j-1)) + f_2(j).(f_1(j,j-1)-f_1(j-1,j)).$$

It is safe to start the procedure in two points where both f_1 and f_2 are negative, for example in $F_1^0 = F_2^0 = 3$ and $F_1^1 = F_2^1 = 2$ and continue until $(F^j - F^{j+1}) < 10^{-5}$.