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Modelling Cod Migration from Greenland to Iceland

by

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Abstract : Migration of cod between West Greenland, East Greenland and Iceland has been modelled, and simulation runs with two models are compared with observed tag return distribution from taggings made in Greenland in the 1955-64 period. The results suggest that the migration can be described as a stepwise migration from West Greenland to East Greenland and then further to Iceland.

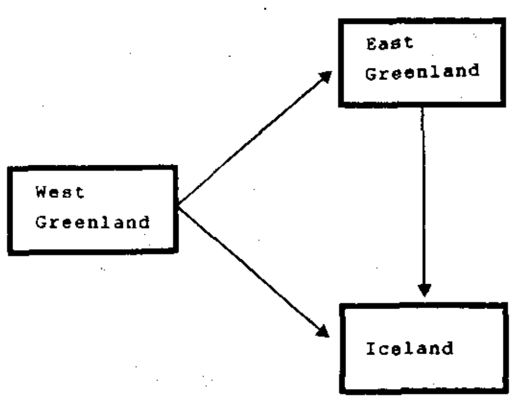
1. Introduction

Harden Jones (1968) reviewed the available information on cod migration between Greenland and Iceland and concluded that a migration from both West and East Greenland to Iceland takes place. The reverse migration, i.e. from eastern to western areas are found not to be of a significant magnitude.

The exact way in which the migration interrelates the three stocks in question is, however, not known. As it is a one-directional west to east migration only two migration models seems however plausible :

1) A linear 3-box model where cod moves from West Greenland to East Greenland and then further to Iceland, i.e.

2) A triangular 3-box model where cod moves to Iceland either directly or via East Greenland, i.e.



In this paper we examine these two models by simulating migration and comparering simulation results with observed recapture information from all three areas.

2. Material and Methods

Tag return data

Table 1 summarizes returns from taggings made in both West- and East Greenland aggregated in five years periods. Only returns af cod tagged at an age of 5 or older are included. 70% of the total recaptures could be directly aged as otolits were submitted, the remaining part was given an age in accordance with an overall age-length key. Recaptures from the tagging year are excluded and this implies that only recaptures of age 6+ are used. This age is chosen as full recruitment to the fisheries occurs at age 6.

For West Greenland returns are available for the entire period 1945-84 although experiments with large numbers of returns exists only for the period 1950-64. The returns from East Greenland only covers the period 1955-64 and 1980-84 and are generally few as not many cod were tagged in this area. As this work requires concurrent returns from West Greenland, East Greenland and Iceland only data from the period 1955-64 can be used.

The majority of tagging experiments took place during summer (more than 95% between May and September- see Hovgård and Christensen, 1988). The time distribution of returns within the year differ, however, greatly between the three areas, reflecting fleet behavoir. At West Greenland the summer fishery was most important, whereas fishing at both East Greenland and Iceland was strongest in the first half of the year (Fig. 1). The pattern seen in Iceland reflects the pronounced spawning fishery at the south-western coast in spring. The East Greenland patterns of returns are less well understood although the cessation in May can be related to the occurrence of actic drift ice. In this work we will, however, pool all returns by calendar years.

A listing of the returns by year after tagging for the two 5-year periods considered (1955-59 and 1960-64) is given in Table 2.

Problems in interpreting tag returns

Interpretation of tag returns is impeded by various kinds of systematic errors. Ricker (1975) classifies these errors in two groups :

A-errors are caused by mortality associated with the tagging and by incomplete reporting of tags. These errors affect the number of returns but not the pattern of returns and, it is hence possible to calculate total mortality from tag returns.

We expect that the reporting of tags in the three areas in question can be quite different and have, therefore, chosen to work only on the return pattern, i.e. the proportion of tag returns in successive years.

B-errors occur if tags are lost at a steady instantaneous rate, either by a physical loss of tags or by an over-death associated with the tags. In this case the estimated Z will reflect the mortality of tagged fish only and not the true Z in the population. Ricker (op. cit) suggests that the size of B-errors should be evaluated by comparing Z's from recaptures with Z's estimated from catch curves.

Catch curve Z's from West Greenland were calculated from catch at age data compiled from Schumacher (1971), Horsted et. al. (1984) and Anon. (1989). These calculations were done on a year-class basis (i.e. diagonally down the catch at age matrix) using only age groups 6-10 in order to exclude the not fully recruited younger fish and the older fish which might be poorly estimated due to their scarcity. Estimations of Z's from tag returns were made after pooling tagging experiments by 5-years periods.

Modelling the recapture pattern

A simple time discrete model is constructed to simulate migration and recapture pattern. The model contains three populations inhabiting West Greenland, East Greenland and Iceland, respectively (fig. 2). Each population is subject to natural mortality (M), fishing mortality (F) and migration 'mortality' (E). The numbers lost due to these mortalities over a time interval t, are

$$\text{Catch} = (F/Z) \times (1-e^{-Zt}) \times N = f \times N$$

$$\text{Nat. deaths} = (M/Z) \times (1-e^{-Zt}) \times N = m \times N$$

$$\text{Migrants} = (E/Z) \times (1-e^{-Zt}) \times N = k \times N$$

The migrants are introduced to the recieving areas in discrete steps. The migrants leaving West Greenland are split up in two groups. One fraction (alfa) is routed to East Greenland while the rest (1-alfa) is routed to Iceland. Using alfa=1 all fish can be routed from West Greenland through East Greenland into Iceland i.e. resulting in a 3-box linear model. Using 0<alfa<1 a 3-box triangular model emerges.

The model is written in DYNAMO and is run with 48 time steps per year. An account of the numbers caught and those that die due to natural mortality are kept for all three areas. In starting the model a stock of 1000 cod tagged 1st of July at West Greenland is used. By trial and error different values of mortality and migrations are applied until the return distributions calculated for East Greenland and Iceland closely resembles the observed ones.

A drawback with this model is that it requires input of seven parameters M, F_w, E_w, F_e, E_e, F_i and alfa (assuming an universal M and no migration out of Iceland) and hence gets very flexible. However, some simplifications can be made by considering some features of catch curves.

Factors influencing the shape of catch curves.

The timely distribution of tag returns is commonly used to calculate total mortality (Z). The numbers caught annually usually declines exponentially and Z is determined by regressing ln(recaptures) vs. time.

If some tagged fish migrate at an instantaneous rate to another area then the recapture pattern will not show an exponential decline with time in the new area as this area recieves new migrants continously. However, the shape of the recapture pattern will depend only on the Z's in the two areas. An instantaneous emigration implies that the number migrating is proportional to stock size, i.e

$$\text{Migrants} = k \times N_t \qquad (N_t = \text{stock size})$$

As $N_t = N \times e^{-Zt}$ it is clear that the number of migrants in any period is simply a scaling of the stock size at the time. Varying the migration rate (k) will not affect the time pattern of migration, although, of cause the absolute magnitude.

The number of recaptures in the new area at any time is likewise

$$\text{Catch} = f \times N_t$$

i.e. the number recaptured is a scaling of stock size. The stock size at any time is dependent of input (which is a scaling of the stock size in the first area and hence a function of Z_1) and decay in area 2 (i.e. Z_2). In total the recapture distribution in area 2 is dependent only on Z_1 and Z_2.

This is illustrated by calculating the return distribution in the recieving area under four sets of varying values of fishing mortality and migration coefficients, but with uniform levels of Z's (Table 3).

These considerations can be extended to cover migration between three areas. In this case (i.e. what we name a 3-box linear model) the return pattern in area three will be dependent on only Z_1, Z_2 and Z_3. These findings facilitate simulations as it is not necessary to make assumptions about the sizes of F's E's and M's as long as their sum is constant and their relative contributions are maintained during the experiment. This simplification is only valid because we restrict our interests to the return pattern in time and hence exclude information on the actual numbers returned (which is exactly what one is doing when determinig Z's from simple catch curves).

Estimations of Z's

The calculation scheme is slightly different for the linear and triangular model.

In the linear model the procedure is to

1. Determine Z_w from a catch curve of recaptures in the tagging area.

2. Run the simulation model with this Z_w and a range of Z_e's.

3. Select that value of Z_e which results in a return distribution which resembles the observed return distribution best.

4. Run the model with Z_w and Z_e for a range of Z_i's.

5. Select the best value of Z_i.

In the triangular model Z_w and Z_e are estimated as above. The return distribution in Iceland will, however, depend on three other parameters :

1) The fraction of migrants from W. Greenland passing through E. Greenland (alfa).

2) The size of the emigration from E. Greenland to Iceland (E_e)

3) The size of total mortality at Iceland (Z_i).

In the simulation, values of E_e are guessed and combinations of alfa's and Z_i's which creates a resonable fit to the observed return pattern are sought.

3. Results

Estimation of Z's at West Greenland

The return distribution of tags and the calculated Z for West Greenland taggings for all 5 year periods since 1945-49 is shown in Table 4 and compared to the Z's determined from catch curves in Fig. 3. The catch curve Z's increases from the start of this timeseries in 1956 and until the late 60'ies from when on it stabilizes at a level of 0.9. Z's from the tag returns are increasing steadily until 1965-69, whereafter a reduction is seen. The general increase in Z up to 1970 has previously been documented both from tag return data (Horsted, 1969) and catch-at age data (Schumacher, 1971). The reduction seen in the Z's from taggings after 1970 does, however, not agree with other findings (see for instance Horsted et. al. 1984). It should be noted that the Z's from tag returns after 1970 are based on very few observations (Table 4).

When looking at the period 1955 to 1969 (Fig 3), i.e. the period when the Z-values determined from returns are based on high numbers of recaptures these Z's are approximately 0.5 higher than the Z's calculated from the catch-at-age data. We attribute this difference to B-errors, i.e. continous tag-loss or over-death of tagged individuals.

If the tag-loss alone accounts for a mortality of 0.5 then the Z for 1945-49 of 0.5 must be estimated wrongly. This is not unreasonable as catches in the decade after WW 2 skyrocked from almost nil to 300.000 tonnes a year. Effort and hence fishing mortality must have increased dramatically and this will lead to an underestimate of Z's from the catch curve on tag returns.

In the simulations the values of 0.83 and 1.08 is used for the periods 1955-59 and 1960-64, respectively.

Estimation of Z's on East Greenland

For East Greenland, Z for the period 1955-59 has been directly calculated from tagging experiments made on East Greenland in this period (Table 2) i.e. by linear regression of ln(recaptures) vs. time. The value of Z found in this way is 0.83 ± 0.20. Data for the 1960-64 are to few for justifying this procedure.

Z's for East Greenland have further been calculated by simulating the observed distribution of recaptures at East Greenland from West Greenland taggings. For the periods 1955-59 and 1960-64 (Z_w's being 0.83 and 1.08, respectively), choises of Z_e's of 0.7 (1955-59) and of 1.3 (1960-64) give good descriptions of the observed return distribution (Fig. 4). The Z for East Greenland found in this way for the 1955-59 period is within the 95% confidence interval of the Z determined directly on East Greenland tagging experiments in the same period.

Estimation of Z's on Iceland

Linear model

In this scenario fish migrate from West Greenland to East Greenland and further on to Iceland. The simulation requires Z_w data from West-Greenland and Z_e data from East Greenland. The input parameters used are :

1955-59	$Z_w = 0.83$	$Z_e = 0.83$
1960-64	$Z_w = 1.08$	$Z_e = 1.3$

The best description is achieved with Z_i's of 1.4 in both periods (Fig. 5) and in both cases the model produces a return pattern closely resembling the observed return distribution.

Triangular model

Before actually working with the triangular model it is illustrative to evaluate a situation with cod migrating directly from West Greenland to Iceland (i.e. a linear 2-box model). This model does not produce realistic return patterns as the typical domed shaped pattern observed in Iceland can not be reproduced (Fig. 6). To create this type of a return curve some delays of entry into the Icelandic area is necessary. One way of achieving this is to apply a much lower Z in West Greenland. This can, however, hardly be justified as the estimates of Z_w's are based on high numbers of recaptures (table 4) and are relative precisely determined.

The other way to delay migration into Iceland is to diverge some cod through East Greenland, i.e. the triangular model. The proportion diverged must be high as delays also implies that these fish are subject to high mortalities (M+F+tag loss). Small fractions routed through East Greenland will hence not seriously change the pattern shown on fig 6. For the same reason E_e must also be high.

In the simulations, values of E_e of 0.1 and 0.5 have been used for 1955-59 and 1960-64, respectively. These values are almost as high as possible considering the restrictions existing (knowledge of Z_e, M=0.2 and tag loss=0.5).

For the 1955-59 period it is only possible to produce recapture distributions close to the observed ones if the proportion routed through East Greenland is in the size range of 0.95 or above. This is to be expected with the quite low value of E_e. The 1960-period is more interesting with its higher E_e. However, even for this period the model fits the observations better the closer alfa gets to unity i.e. as the proportion routed through East Greenland increases (Fig 7). The best fit is achieved with the following combinations of alfa and Z_i.

Alfa	0.7	0.8	0.9
Z_i	0.7	0.8	0.9

4. Discussion

The simulations show that the best description of the recapture pattern at Iceland is achieved when using a linear 3-box model, i.e. when all fish migrating from West Greenland to Iceland passes through East Greenland. In the triangular model, where some cods migrate directly from West Greenland to Iceland without entering East Greenland, acceptable agreements between simulations and observations are achieved only if this direct migration is small. In this case of course, the triangular model is in effect reduced almost to the linear model.

In the linear model the following Z's have been used.

Period	West-Greenland	East-Greenland	Iceland
1955-59	0.83	0.83	1.4
1960-64	1.08	1.3	1.4

Are these values now realistic ? No other estimates of Z are available for East Greenland. For Iceland F's from 1963 to 87 have been calculated by VPA assuming M=0.2 and no migration out of the area (Fig. 8). F for 63-64 is around 0.6. Adding

M=0.2 and a "tag loss" of 0.5 leads to a Z of 1.3 i.e. the same magnitude as the Z determind for the model. Thus, when assuming a tag loss of the magnitude of 0.5 the linear 3-box model predicts reasonal levels of Z in Iceland.

Use of the model

In the linear 3-box model it is possible to give analytical expressions of the total numbers of recaptures expected in all three recapture areas from taggings carried out in West Greenland if the reporting rate are known. (se Appendix).

If assuming that the reporting rates were the same in East Greenland and Iceland it is possible to express the emigration rate at East Greenland as a function of F at East Greenland :

$$E_e = F_e \times (R_i/R_e) \times (Z_i/F_i)$$

where R_i, R_e are total returns in East Greenland and Iceland from a tagging experiment at West Greenland. Using the observed R_i/R_e = 2 for the 1955-64 period and a Z_i=1.4 and F_i=0.7, this leads to an E four times as large as F. This suggests that the flow of fish through the East Greenland area is much more important for changes in stock size than are the fisheries. This is in agreement with the findings of the ICES East Greenland Cod Working Group.

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Tabel 1 Recaptures of age 6+ cod tagged in West and East Greenland aggregated by 5 years periods.

Taggings in West Greenland

Recapture area	West Greenland	East Greenland	Iceland
Years			
1945-49	393	1	34
1950-54	1342	10	122
1955-59	2194	48	116
1960-64	1441	101	193
1965-69	282	14	52
1970-74	59	14	22
1975-79	16	0	10
1980-84	12	2	11

Taggings in East Greenland

Recapture area	West Greenland	East Greenland	Iceland
Years			
1955-59	8	58	143
1960-64	3	8	46
1980-84	1	43	21

Table 2: Tag returns by tagging area, years after tagging and area af recapture for West- and East Greenland taggings, 1955-64.

West Greenland taggings

1955-59

Years after tagging	1	2	3	4	5	6	7	8	9	10
Return area										
West Greenland	1272	513	236	84	59	16	11	3	0	0
East Greenland	12	14	9	5	5	2	1	0	0	0
Iceland	20	32	29	18	12	3	2	0	0	0

1960-64

Years after tagging	1	2	3	4	5	6	7	8	9	10
Return area										
West Greenland	893	313	157	51	20	6	1	0	0	0
East Greenland	47	29	14	6	4	1	0	0	0	0
Iceland	44	67	45	30	7	0	0	0	0	0

East Greenland taggings

1955-60

Years after tagging	1	2	3	4	5	6	7	8	9	10
Return area-										
West Greenland	2	2	2	2	0	0	0	0	0	0
East Greenland	27	17	10	3	1	0	0	0	0	0
Iceland	40	52	30	16	3	2	0	0	0	0

1960-64

Years after tagging	1	2	3	4	5	6	7	8	9	10
Retutn area										
West Greenland	1	0	1	1	0	0	0	0	0	0
East Greenland	3	3	2	0	0	0	0	0	0	0
Iceland	17	15	11	2	1	0	0	0	0	0

Table 3: Four simulations of numbers caught per year in area two which recieves migrants from area one. 1.000 fish is assumed taged at 1. January year 1 in area 1.

Model parameters

RUN	M	F_1	E_1	Z_1	F_2	E_2	Z_2
1	0.2	0.4	0.1	0.7	0.3	0.4	0.9
2	0.2	0.4	0.1	0.7	0.1	0.6	0.9
3	0.2	0.3	0.2	0.7	0.5	0.2	0.9
4	0.2	0.3	0.2	0.7	0.7	0	0.9

Recaptures in area 2

YEAR	1	2	3	4	5	6	7	8+	Total
Run									
1	8.828	13.371	10.293	6.596	3.880	2.172	1.178	1.293	47.61
2	2.943	4.457	3.431	2.199	1.293	0.724	0.393	0.431	15.87
3	29.43	44.57	34.31	21.99	12.93	7.24	3.93	4.32	158.72
4	41.20	62.40	48.03	30.79	18.10	10.14	5.50	6.05	222.21
%	18.54	28.08	21.61	13.86	8.15	4.56	2.48	2.72	100.00

Table 4: Recapture at West-Greenland from West Greenland taggings by year after tagging, aggregated by 5-year periods. Z calculated by regressing ln(recaptures) vs. year.

Recp. Yr.	1	2	3	4	5	6	7	8	9	10	Z
Tag. period											
1945-49	166	96	62	39	13	8	0	6	3	0	0.50
1950-54	657	330	191	95	44	12	7	4	1	1	0.77
1955-59	1272	513	236	84	59	16	11	3	0	0	0.83
1960-64	893	313	157	51	20	6	1	0	0	0	1.08
1965-69	201	68	12	1	0	0	0	0	0	0	1.76
1970-74	42	14	2	2	1	1	0	0	0	0	0.95
1975-79	9	5	1	0	1	0	0	0	0	0	0.57
1980-84	9	3	0	0	0	0	0	0	0	0	1.09

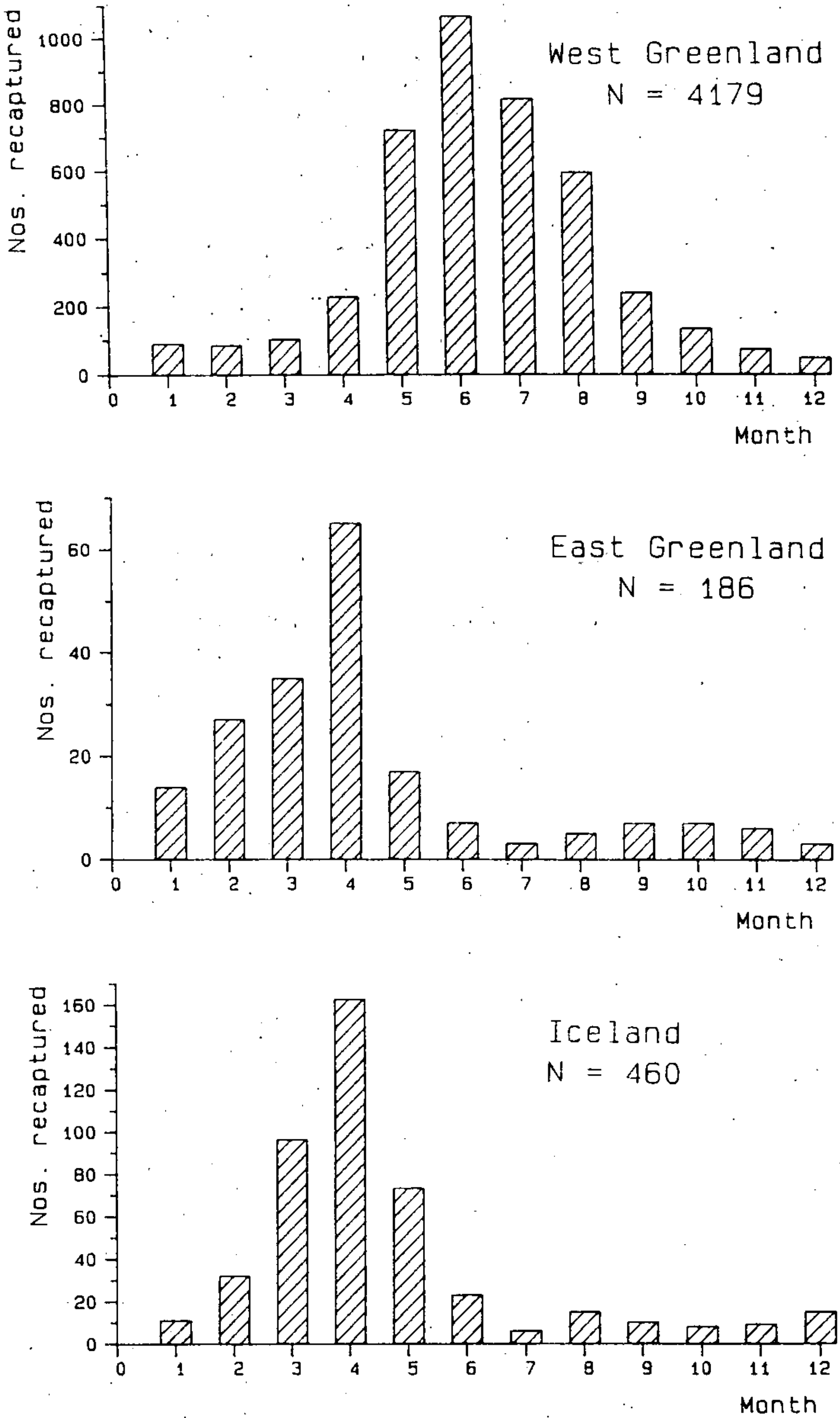


Fig. 1 : Number of recaptures of age 6+ cod by month, in West Greenland, East Greenland and Iceland from Greenland tagging experiments, 1955-64.

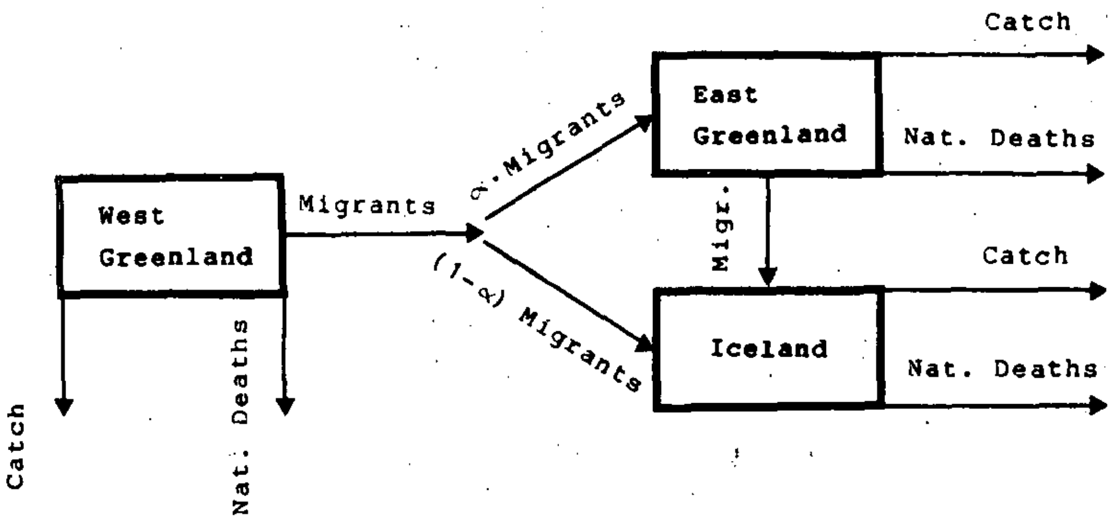


Fig. 2 : Diagram showing the flow of cod used in cunstructing the two simulation models. By choosing alfa=1 (i.e. disconnecting the direct flow between West Greenland and Iceland) a linear 3-box model is made. Otherwise, (0< alfa <1) the model is triangular.

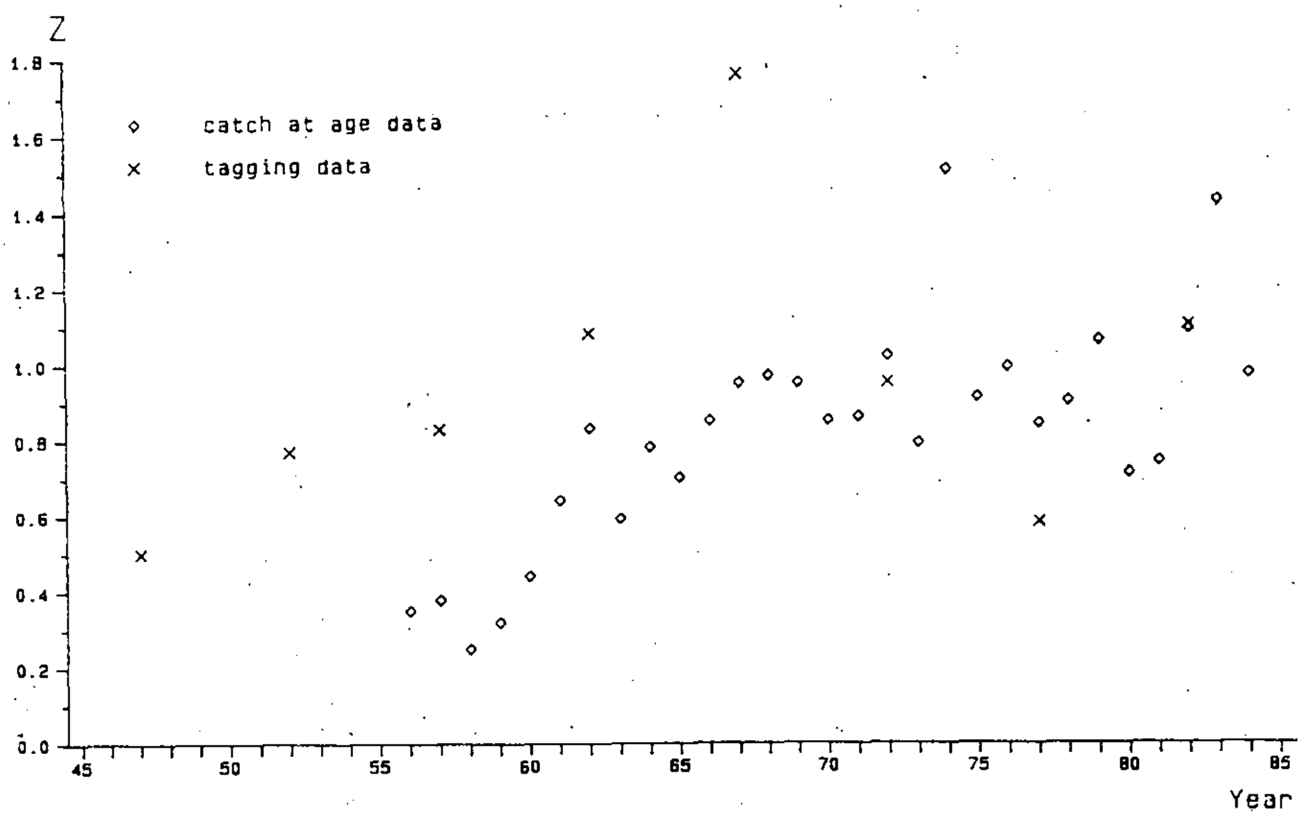


Fig. 3 : Total mortality (Z) in West Greenland, 1945-84, as determined from catch-at-age and tag return data.

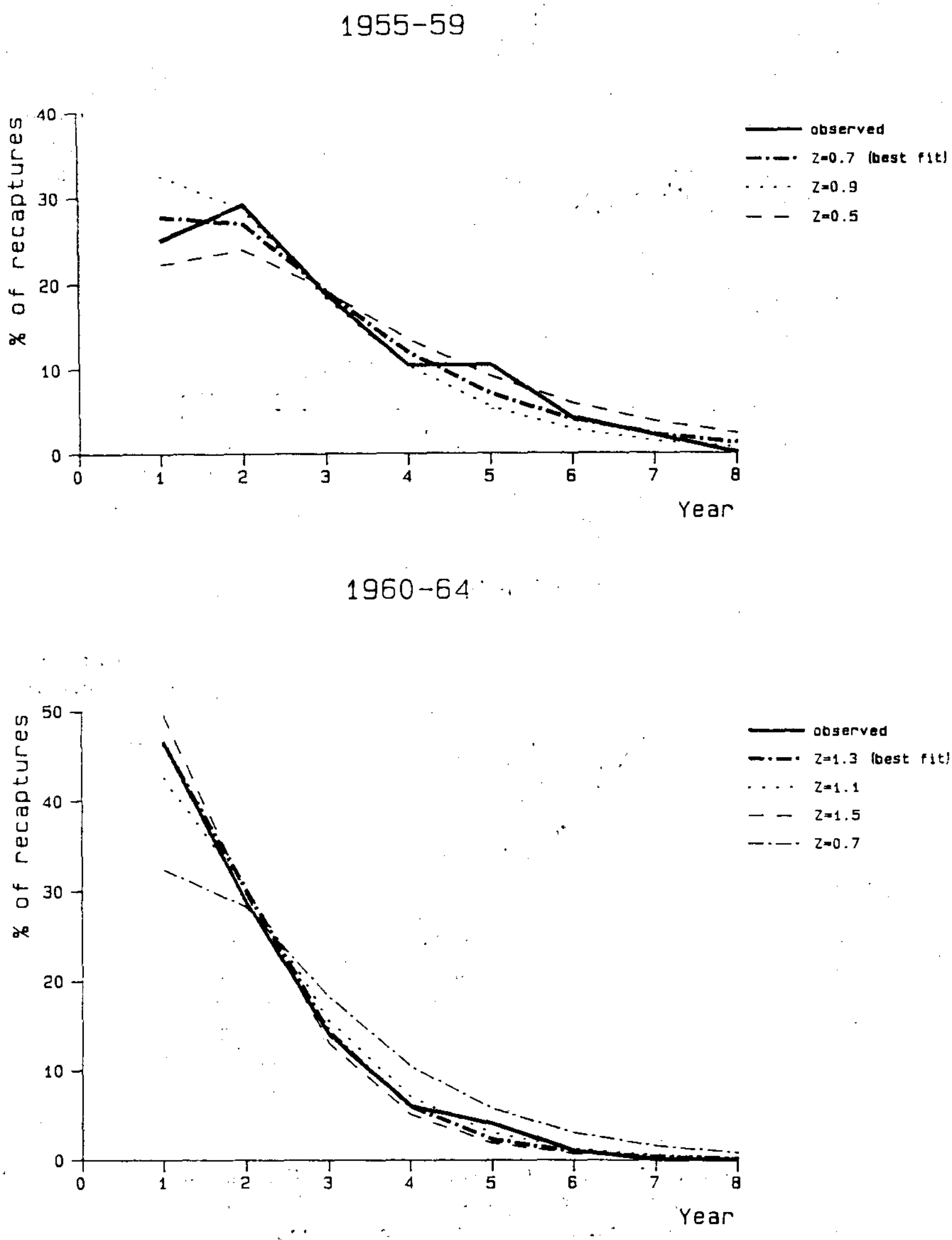
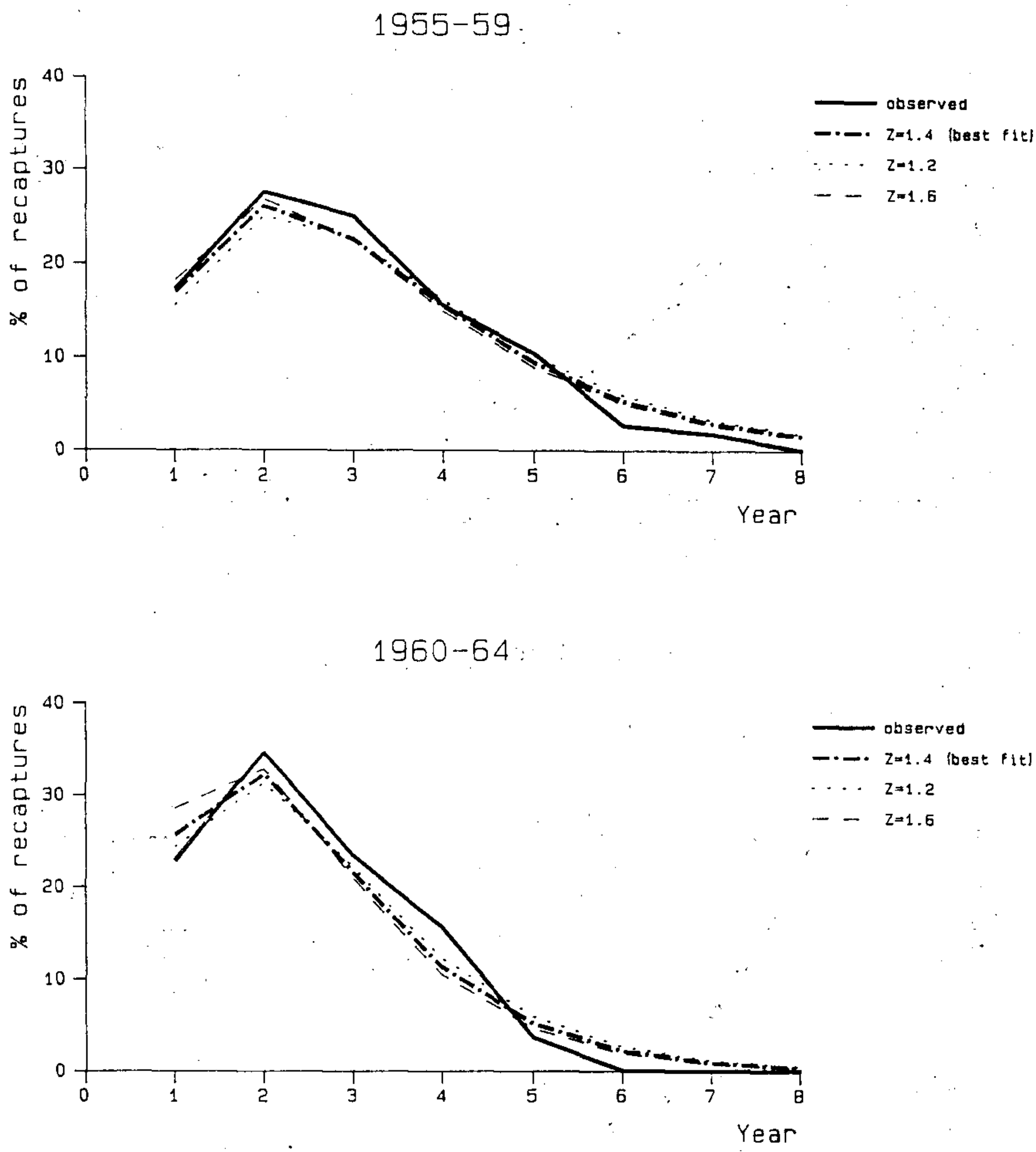
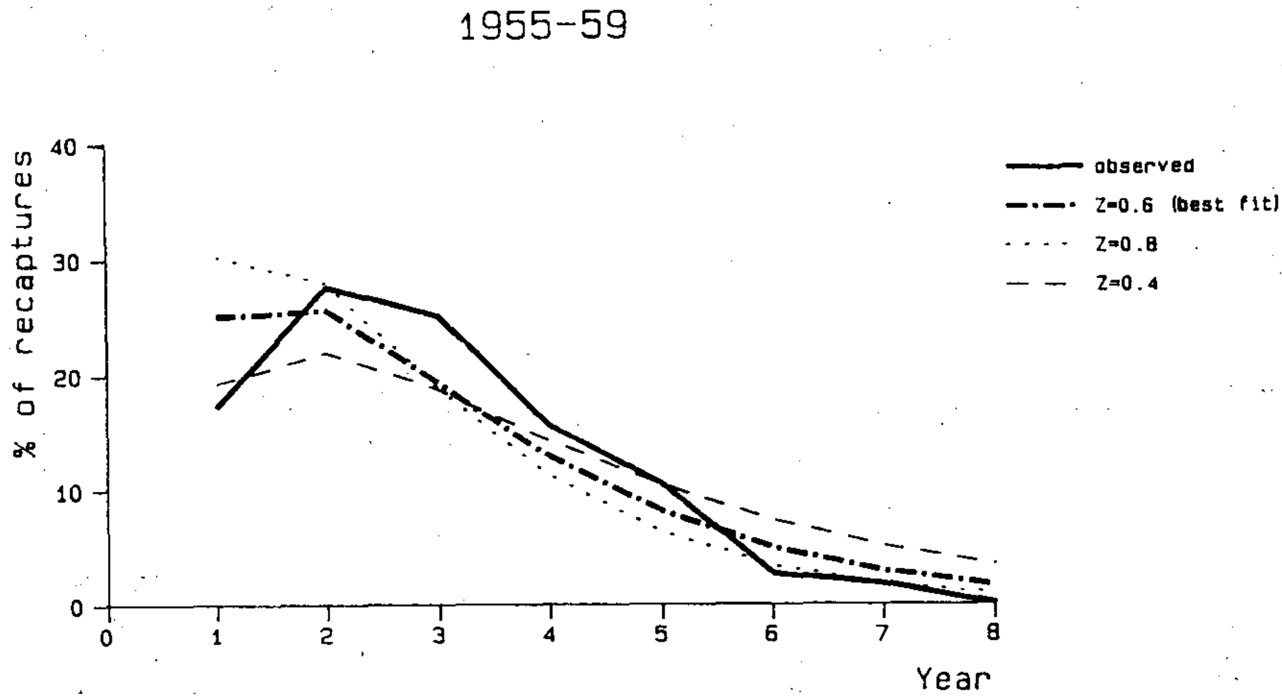
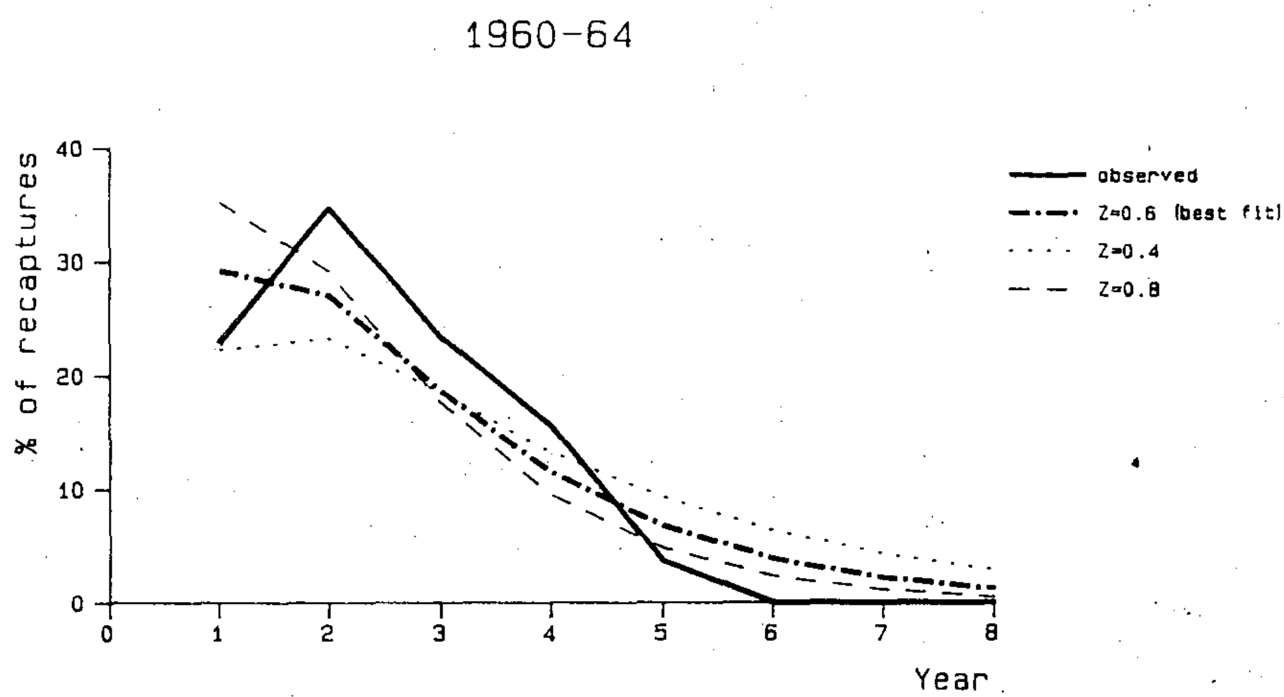


Fig. 4 : Observed tag distribution by year after tagging in East Greenland from West Greenland tagging experiments in 1955-59 and 1960-64 compared to simulated return distributions.

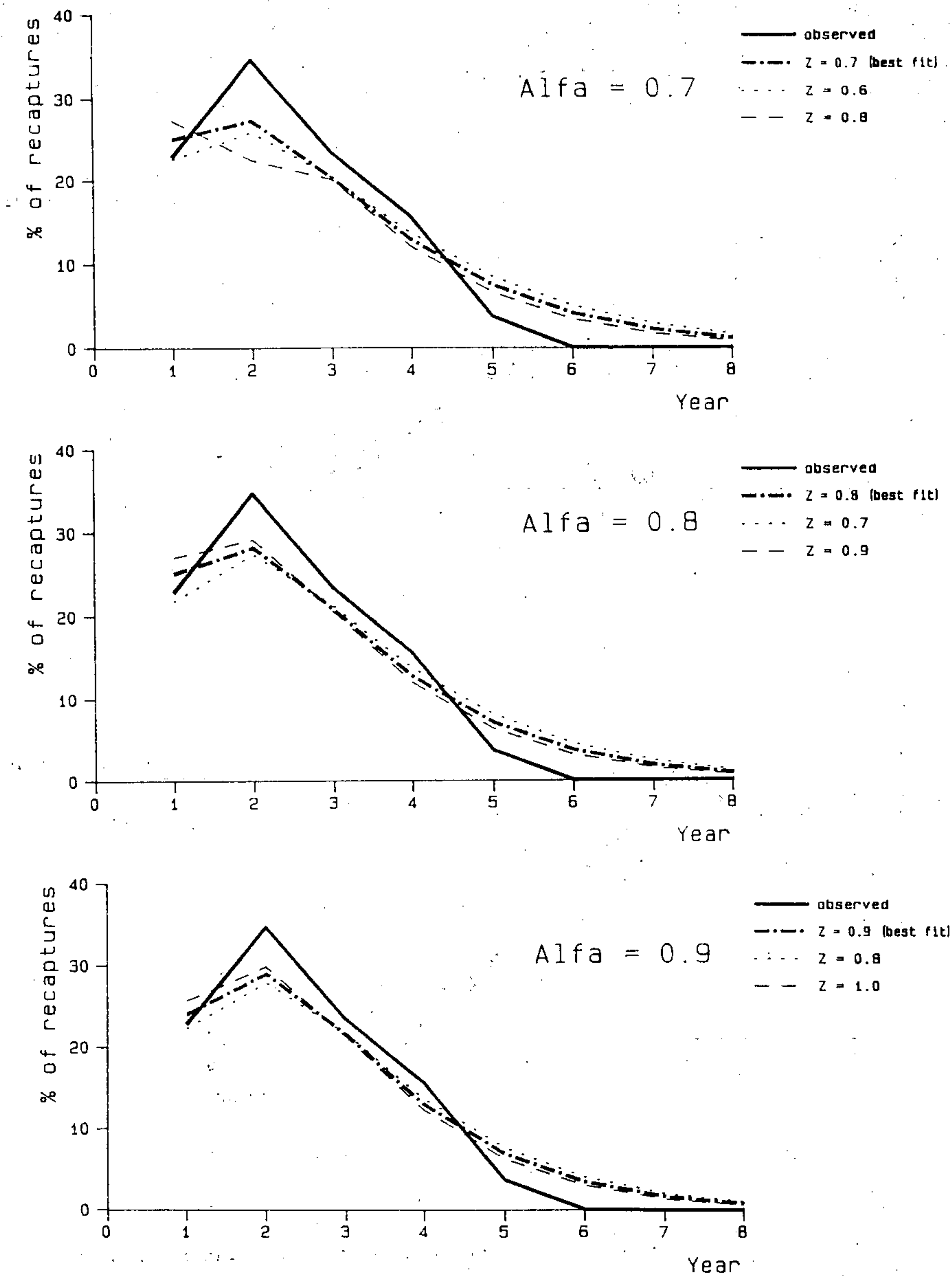


<u>Fig. 5</u> : Observed tag distribution by year after tagging in Iceland from tagging experiments in West Greenland, compared with simulated return distributions from the 3-box linear model.





<u>Fig. 6</u> : Observed tag distribution in Iceland from West Greenland tagging experiments, compared to simulated return distributions from a 2-box West Greenland to Iceland model.



<u>Fig. 7</u> : Observed tag distribution at Iceland from West Greenland tagging experiments, 1960-64, compared to simulated return distributions from the 3-box triangular model. Alfa is the proportion of West Greenland migrants that are routed through East Greenland (se Fig. 2).

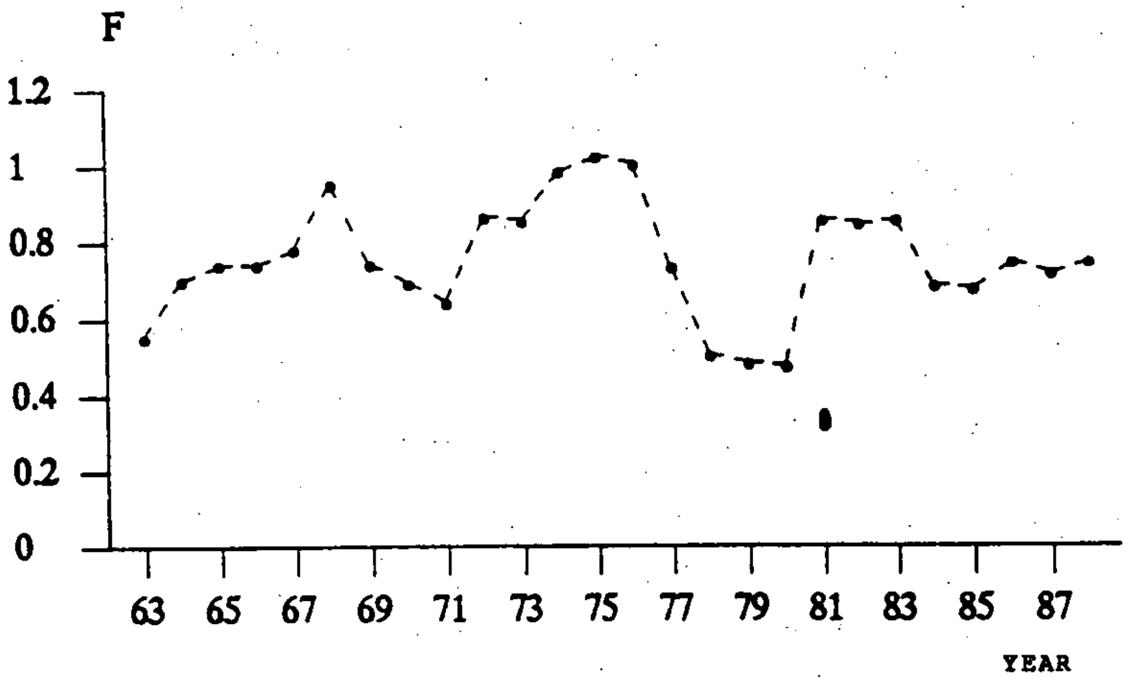


Fig. 8 : Fishing mortality (F) at Iceland, 1963-88), as determined by VPA. Data from Anon., 1988.

Appendix

Some simple expressions of expected returns in the 3-box model

In a tagging experiment the total numbers of expected returns can be expressed as :

$$R = a \times N \times (F/Z)$$

where R designates the total number of returns over time, a is reporting rate of returns, N is number of tag releases and F and Z are fishing- and total mortality, respectively. When fish are migrating at an instentanous rate through different areas some simple extensions of this relationship can be deducted.

Using the indices w, e, i, for W. Greenland, E. Greenland and Iceland, respectively, the numbers of expected returns in the three areas from tag releases at West Greenland can be expressed as :

(1) $$R_w = a_w \times N \times (F_w/Z_w)$$

(2) $$R_e = a_e \times N \times (E_w/Z_w) \times (F_e/Z_e)$$

(3) $$R_i = a_i \times N \times (E_w/Z_w) \times (E_e/Z_e) \times (F_i/Z_i)$$

Use of these expressions are impeded by the lack of good information on the size of the reporting rates. For West Greenland, at least, we think that the reporting rate is quite dependent on fleets (Horsted, 1963) and that it has changed markedly during the post war period.

The expression used in the last section of the paper is derived by assuming that $a_e = a_i$ and then rearranging equations (2) and (3).