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The Assessment of the Migration of Atlantic Cod (*Gadus morhua* L.) between the Stocks off East and West Greenland by Means of Otolith Typing

by

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Abstract

The purpose of this article is to analyze the influence of Greenland cod migration to the stock assessments carried out by the ICES and NAFO working groups on cod stocks off East and West Greenland. A method is described which enables the identification of the adolescent areas of West and East Greenland with an error of 20 % on individual basis. The single annual growth zones in the cod otoliths (sagitta) were classified to three different types and used as natural tags. No indication of a genetically determined formation of the different annual growth zones could be proved due to the very low amount of genetic differentiation among the sympatric stocks of Atlantic cod. On the contrary the study points to the fact that the different hydrograghic conditions of the nursery grounds affects the growth of the cod. So the hydrographic conditions are manifested as natural tags in the form of different annual growth zones in the otoliths.

The procedure for the identification of the adolescent areas on individual basis offers the recalculation of the population dynamics of the cod stocks off East and West Greenland. The computation of the emigration and immigration rates confirms the concept of the Greenland cod migration derived from tagging experiments. In 1984-86 a very numerous and rapid emigration of the cod of the fully recruited cohorts from West to East Greenland occurred. The coefficient of emigration E of the West Greenland cod stock increases with age to 0.65. So the immigrants of the East Greenland cod stock originating from West Greenland contribute as many as 75 % of the total year class strength of older ages. The analysis of the migration pattern shows that in 1984-86 mature cod did not migrate from East to West Greenland. Regarding the West Greenland stock the results suggest an increased number of immature cod emigrated from East Greenland. The paper proposes the incorporation of the findings into the standard assessment method applied by the ICES and NAFO working groups on cod stocks off East and West Greenland.

Introduction

Since 1931 (Schmidt, 1931) it has been recognised from extensive tagging experiments that some mature cod migrate from West to East Greenland and further to the spawning grounds at the Icelandic continental shelf. This may also be sometimes the case for immature cod originating from the East Greenland area in close vicinity to Iceland (fig. 1). Against this easterly direction a migration of mature cod from Iceland to Greenland waters hardly occurs (Hansen, 1949). Therefore, the migration of mature cod from Greenland waters to Iceland can be regarded as a one-way emigration (Anon., 1973).

However, the working groups of the International Council for the Exploration of the Sea (ICES) and the Northwest Atlantic Fisheries Organization (NAFO) on cod stocks off East and West Greenland designate the interrelation between these cod stocks as a complex (Anon., 1986). Particularly as on easy hydrographical conditions a larval drift with currents from Iceland to East and West Greenland seems evident (Hovgard and Messtorff, 1987). The variation of the contribution of this larval drift to the recruitment of the cod stocks off East and West Greenland is reflected by the abundance indices from the Icelandic 0-group survey (Vilhjalmsson and Magnusson, 1986).

At the present the stock assessment of the cod stocks off East and West Greenland, which are of great importance for the German fishery (Schumacher, 1986), are carried out separately. This results essentially from scientific groundfish survey programmes designed and introduced by the Federal Republic of Germany at the beginning of the 1980 decade. The ICES and NAFO working groups pay attention to the importance of the cod migration in their reports by using a coefficient of emigration E varying between 0.05-0.29.

Due to the fact that quantitative information on fish migration is not derivable from tagging experiments (Harden Jones, 1968) the investigations are concentrated about the usability of the cod otoliths as a natural tag. The identification and separation of fish stocks by means of the calcified structures of their individuals have been used frequently in fisheries biology (Ihssen et al., 1981). Additionally the otolith readers of the Institut für Seefischerei (Hamburg) and the Greenland Fisheries Research Institute (Copenhagen) pointed to typical otolith structures of cod caught at East and West Greenland. Hence a method of otolith typing is elaborated by an international working group with the participation of scientists and technical assistants of both institutes.

The application of the otolith typing offers the identification of the adolescent areas on individual basis and the assessment of the cod grown up within a stock unit separated from the immigrants. On this basis a recalculation of the population dynamics of the cod stocks off East and West Greenland is carried out. Thereby directly estimated emigration and immigration rates are included.

Topography and Hydrography of Greenland Waters

The area of the North Atlantic Ocean around Greenland was an object of scientific investigations since the middle of the last century at irregular intervalls. Hansen (1949), Dunbar (1951), Dietrich (1957) und Stein (1987 b) give an account of the historical development of the oceanographic exploration in this area. Because of the depth related occurrence of the cod (Sahrhage, 1980; Messtorff, 1980; Messtorff and Wagner, 1980; Messtorff and Kosswig, 1986), which is limited to the 600 m isobath, only the relative narrow oceanic shelf of Greenland is of interest. Here, small banks are formed by steep canyons making the Greenlandic shelf a very difficult area for a groundfish survey and the commercial fishery (fig. 3 and fig. 4).

The hydrographical conditions in the western part of the Irminger Sea and the Denmark Strait between East Greenland and Iceland are influenced by two currents flowing southwards to the Cape Farvel (Dietrich, 1957). The East Greenland Current originates from the Greenland Sea and flows near the coast of East Greenland southwards over the Greenland-Iceland Sill to the Cape Farvel (fig. 2). It consists only of Polar water ranging from -0.5°C to -1.0°C in temperature and from $33.00 \cdot 10^{-3}$ to $33.75 \cdot 10^{-3}$ in salinity (Müller et al., 1979). Drifting in this cold water even

icebergs and pack-ice arrive the East Greenland waters, particularly from December until June (Stein, 1987b; Meyer, 1964). The latter is called Irminger Current and a branch of the North Atlantic Current. The near bottom layer of the offshore banks is mainly under the regime of the warm Irminger Current with the Irminger Sea water (4 °C, 34.97*10^{-3}), North Atlantic water (7 °C, 35.10*10^{-3}) and Labrador Sea water (3.8 °C, 34.88*10^{-3}).

Also the Irminger Current flows southwards in parallel to the East Greenland Current. From observations of the climate it is known that the mixing process of these two currents results in meandering cold and warm bands, making the environmental conditions in this area rather changeable. Variations in temperature of 5 °C are possible during a period of 3 days (Stein, 1987 a). Additionally an outflow of cold Greenland Sea water exists (Ross and Meincke, 1979). Mann (1969) and Stein (1974) describe an inconstant overflow of very dense water close to the bottom which renews the deep layers of the Irminger Sea.

The West Greenland Current flows northwards from the Cape Farvel to the Davis Strait and the Baffin Bay. Its water originates partly from the cold East Greenland Current and partly from the warmer Irminger Current. As it flows northwards the original characteristics of the water masses are lost more and more (Buch, 1984). Consequently the hydrograghic conditions in the West Greenland area are much uniformer than in the East Greenland area.

Only the upper water layer (0-50 m) is slowly heated by solar radiation from -0.5 °C to 4 °C in July-October and affected by short-term atmospheric changes (Stein and Buch, 1984).

The deeper water layers off the west coast of Greenland show a distinct annual periodicity in the intensity of the inflow of the water masses. The cold Polar water of East Greenland origin dominates during spring, whereas the warm Irminger component of the West Grenland Current intensifies its input of heat during the summer and autumn, reaching its peak at a temperature of 4 °C in December. At the rest of the year the temperature ranges only from 1 °C to 3 °C (Buch, 1982). Water of Atlantic origin dominates at depths greater than 400 m troughout the year (Stein and Buch, 1985).

Since their systematic exploration the hydrographic conditions of the West Greenland waters showed strong anomalies at irregular periods (Hansen, 1949). The year to year variations are mainly correlated to the relativ strengths of the East Greenland and the Irminger Current as well as the meteorological situation. In 1980-84 extreme cold arctic air masses caused a strong cooling of the upper water layers, while in 1984-86 the temperature of the atmosphere returned to normal. So even positive temperature and salinity anomalies were observed during this time (Stein, 1986 a and 1987 c; Buch, 1986).

Materials and Methods

The Stock Assessment

The investigation of the migration of the cod is limited to 1984-86. As data of the commercial fisheries do not adequately reflect the status of the cod stocks off East and West Greenland, annual groundfish surveys were introduced by the Federal Republic of Germany in order to obtain estimates of the biomass and abundance of cod in both areas. The total survey time extends from September till the beginning of December. About 150 hauls were carried out in each area using the "140 foot bottom trawl" equipped with a small mesh liner (30 mm) inside the codend. The horizontal net opening amounts to 22 m, the vertical net opening to 3.5 m headline height. As a rule the trawling speed is 4.5 knots and the towing time lasts 30 minutes. Fishing is conducted between 6 o'clock a.m. and 8 o'clock p.m.

The survey areas off East and West Greenland are shown in fig. 3 and fig. 4 respectively. The hauls are randomly selected covering the whole survey area excluding the 3-mile zone. The East Greenland area as well as the West Greenland area consists of different numbers of strata which are subdivided by 200 m depth zones down to 600 m. For detailed informations on survey design, strata boundaries and strata areas see Anon. (1987), Messtorff and Cornus (1984) and Rätz (1989).

The assessment of the stock biomass and abundance results from the "swept area method" combined with a stratified random sampling system (Cochran, 1977; Saville, 1977). The catchability coefficient, the most uncertain factor of a groundfish survey, has been determined to be 1.0 by the working groups regarding the estimates as the "minimum trawlable" biomass and abundance.

In contrast to the estimates of the cod stock off West Greenland, which are received from the NAFO working group (Schumacher, 1987; Horsted, 1986; Cornus et al., 1985), the values of the biomass and abundance of the cod stock off East Greenland from 1984-86 are recalculated (tab. 7, 8, 9, 10). During this period the ICES working group used assessments derived from a stratification based on the density distribution of cod within statistical rectangles (Cornus, 1984 and 1985; Anon. 1985, 1986, 1987). As the abundance of the cod off East and West Greenland depends not only on the geographic latitude and longitude but also on the depth and some other biological facts this procedure led to misrepresentations (Rätz, 1989). Therefore the survey data are restratificated and assimilated to the assessment method of the NAFO working group. Depth stratifications are going to win recognition concerning the design of groundfish surveys (Bowering, 1987 a and b).

Theory of Emigration and Immigration

The first and most important step of stock assessments is the clear definition of the exploited stock unit and its limitations by means of biological parameters or the kind and structure of the fishery (Gulland, 1983). Unfortunately the great majority of the mathematical models evolved and used in fisheries biology is valid only with the restriction that individuals neither leave the stock unit nor join it. This fact arises from the ignorance of the multifarious mechanism causing and stimulating the fish migrations.

Though Beverton and Holt (1957) consider the migration of immature individuals from their adolescent areas to the spawning stock, but these adolescent areas are included in the whole living space of the stock unit. Consequently they describe the transport of individuals as a function of the initial stock. In this model the expected strength of the immigration is determinded by the status of the initial stock. Ricker (1975) regards the emigration of individuals out of the stock unit by the summation of the emigrants to the total stock mortality. So he defines an instantaneous rate of total loss of individuals. This approach is adopted in the calculation model of the emigration in contrast to Ulltang (1977). He considers the emigration as a part of the natural mortality rate and develops the consequences for the virtual population analysis.

Whereas the emigrants belong to the exploited stock and therefore are combined with the total loss of individuals, an immigration happens independent of the analyzed stock. The strength of an immigration is only due to that stock of which the individuals emigrated previously. Hence the immigrants are regarded as an autonomous unit within the analyzed stock following the concept of the ICES working group (Anon., 1987). The mathematical model computes separately the population dynamics of the individuals grown up in the stock unit and the population dynamics of its immigrated component. The separation between these two parts results from otolith typing.

The emigration of mature cod to Iceland is not taken into account (fig. 1). This implies that the terms emigrants and immigrants refer only to the stock units off East and West Greenland. On this assumption the fish migration is limited to the closed system of the areas off East and West Greenland. The schematic illustration of the migration between two stocks considered in the calculation modell is shown in fig. 5. Excluding the returning emigrants it is evident that the number of individuals emigrated out of stock 1 is identical with the number of immigrants of stock 2. Analogous the same finding is valid for the number of individuals immigrated into stock 1 which are originating from stock 2. The calculation model is based on the identification of the immigrants within both stocks by means of their otolith structures. Thereafter the numbers of immigrants are inserted into the population analysis of the respective stocks as the numbers of emigrants.

The loss of individuals of a single fully recruited year class is represented by means of an exponential function (fig. 6). The function of the loss of individuals grown up in the stock unit f(N) is overlaped by the function of the loss of immigrants f(I) if an immigration happened till time 0. So the function f(N+I) shown in fig. 6 describes the total loss of individuals in the stock unit in the case that no more immigrants join the stock from time 0 till 1. This period is determined to be one year for this example. A continuous immigration f(I) over this time is quite another matter and will be discussed later on (fig. 6, spotted line).

The decrease of individuals of a single year class over the period from 0 till 1 is given by the common formula :

(1) $N_1 = N_0 e^{-Z}$

with

N=number of individuals grown up in the stock unit

Z=total mortality

Extended to the intention of a separate computation of the population dynamics of the individuals originating from the stock and its immigrated component the formula (1) one reads :

(2) $N_1 + I_1 = N_0 e^{-Z_N} + I_0 e^{-Z_I}$

with

I=number of immigrants

Z_N=total mortality of the individuals grown up in the stock unit

Z_I=total mortality of the immigrants

Ricker's (1975) concept transforms the total mortality to the coefficient of the rate of the total loss of individuals including the emigration :

(3) $Z_N = M_N + F_N + E_N$

with

M_N=natural mortality of the individuals grown up in the stock unit

F_N=fishing mortality of the individuals grown up in the stock unit

E_N=emigration of the individuals grown up in the stock unit

On the other hand the total loss of immigrants is composed of the natural mortality and the fishing mortality only because the calculation model excludes the returning emigrants :

(4) $Z_I = M_I + F_I$

with

M_I=natural mortality of the immigrants

F_I=fishing mortality of the immigrants

The following formula (5) integrates the definitions of the total mortalities (3,4) within the formula (2) :

(5) $N_1 + I_1 = N_0 e^{-(M_N + F_N + E_N)} + I_0 e^{-(M_I + F_I)}$

Nevertheless a continuous immigration from time 0 till 1 is not taken into consideration so far. As mentioned above the continuous immigration is illustrated as a spotted line f(I) in fig. 6. The instanteneous immigration takes place independent of the initial stock. For that reason the instantaneous immigration I' is appended to formula (5) as an additive variable :

(6) $$N_1+I_1 = N_0 e^{-(M_N+F_N+E_N)} + I_0 e^{-(M_I+F_I)} + I'$$

The formula (6) provides not separately the mortality of the individuals immigrated during the intervall from 0 till 1. The natural mortality M_I and the fishing mortality F_I include this loss already. Consequently the values M_I and F_I are overestimated by the amount of the individuals immigrated and lost from time 0 till 1.

In the following the calculation of the losts of individuals Z, M, F and E as well as the instantaneous immigration I' will be explained from the data collected. The results of East and West Greenland are represented in a tabular form and devided into the two periods from autumn 1984 till 1985 and autumn 1985 till 1986 (tab. 7, 8, 9, 10). The first column of the tables specifies the year classes in order to define each of the lines. The second and third column, called $N_{t1}+I_{t1}$ and $N_{t2}+I_{t2}$, give the strength of the total year classes at the beginning t1 and at the end t2 of the intervall. Using these values and the formula (7) the total loss of individuals Z_{N+I} is calculated and entered into the fourth column.

(7) $$Z_{N+I} = -\ln((N_{t2}+I_{t2})/(N_{t1}+I_{t1}))$$

The second part of the assessment tables gives an account of the population dynamics of the individuals grown up in the stock unit only. The first two columns of the second part N_{t1} and N_{t2} list the number of individuals grown up in the stock per year class at the beginning and at the end of the period. The next column F'_N gives the number of individuals grown up in the stock and died by fishing. These values are adopted from the reports of the ICES and NAFO working groups (Anon., 1986 amd 1987) and split up proportionally to the part grown up in the stock and to its immigrated component at the time t2. The number of individuals emigrated out of the stock during the period can be taken from the column called E'_N. These individuals are identified as the instantaneous immigrants of the second stock and introduced here. The coefficients of the total loss of individuals grown up in the stock unit Z_N are listed in the following column.

(8) $$Z_N = -\ln(N_{t2}/N_{t1})$$

The values of the columns FN and EN (fishing mortality and emigration of the individuals grown up in the stock) are calculated using the formula :

(9) $$F_N = -\ln((N_{t1}-F'_N)/N_{t1}) \text{ and}$$

(10) $$E_N = -\ln((N_{t1}-E'_N)/N_{t1})$$

The natural mortality of the individuals grown up in the stock M_N entered into the last column of the second part of the assessment tables is determined after the transformation of the formula (8) to :

(11) $$M_N = Z_N - F_N - E_N$$

The third part of the assessment tables informs about the population dynamics of the immigrants only. For that purpose the first two columns I_{t1} and I_{t2} give the number of immigrants per year class at the beginning and at the end of the period. The numbers of immigrants died by the fishery are listed in column F'_I. Compared to the individuals grown up in the stock these values are adopted from the reports of the ICES and NAFO working groups. Again the catches are splitted proportionally to the part grown up in the stock and to the immigrated component at the end of the intervall. The fishing mortality of the immigrants F_I is calculable by means of the formula :

(12) $$F_I = -\ln((I_{t1}-F'_I)/I_{t1})$$

The total loss of the immigrants Z_I is not determinable by using the strengths of the year classes I_{t1} and I_{t2} since a continuous immigration during the period increases the number of individuals. Thus the natural mortality of the immigrants M_I is defined to 0.2 for all year classes in order to calculate their total loss of individuals Z_I using the formula :

(13) $$Z_I = F_I + M_I$$

The results of these estimates are entered into the column next to the last. Only the application of the Z_I combined with the strength of the year classes enables the calculation of the number of individuals immigrated during the period from t1 till t2. This procedure results from the formula :

(14) $$I' = I_{t2} - I_{t1}e^{-Z_I}$$

I' represents the strength of the immigration and the objective of the derivations. The values of I' are specified in the last column of the assessment tables.

Material of Otoliths and Handling

Studies of population dynamics necessitate a reliable age determination of the individuals. Hoffbauer (1898) was the first to use scales for age determinations while Reibisch (1899) found out the identification of year classes by means of otolith investigations. Gulland (1958) suggests the otoliths for age determinations instead of scales or fin rays. Beamish and McFarlane (1983) point to the critical fact that at the present only 65 % of the age determinations of fish species carried out world-wide include or refer to a validation study. The validity of age determinations is provable by tagging experiments, growth investigations and the recognition of dominant year classes. Saetersdal (1953) succeeds in demonstrating the interrelation between the growth of the individuals, the time of zone formation of the otoliths and the seasonal environmental parameters. Meyer (1965 b) verifies the age determinations of cod off Greenland by means of recaptures. Additionally the growth analysis (Rätz, 1989) and the identification of single year classes leave no doubt about the accuracy of the age determinations.

From 1984-86 the left and right sagitta of the labyrinthine organs have been collected from 13,200 specimens. The otoliths were stored in small paper-bags labeled with an identity number, morphometric measurements (total length of the specimen in centimetre below, individual weight), sex and maturity. Tab. 1 gives a general view of the total otolith material collected. The otolith sampling was lenght-stratified to ensure the collection of the sagittae of at least 30 specimens per lenght class (3 cm).

Only one of both otoliths has been used for the age determination because different numbers of annual zones in the right and left sagitta are recorded very rarely (May, 1954; Reinsch, 1968). This otolith is cutted across the centre by means of a fine mechanical saw (Meyer, 1965 c). The procedure of otolith sawing results in two almost standard sections with polished surfaces (fig. 7). Both sections are mounted on a small socle of plasticine and examined under a binocular microscope using side illumination. In the otolith the zones of the faster growth appear dark (opaque) while the zones of the slower growth are shining bright (hyaline) in transmitted light. The rate of the growth affects the translucence of the otolith consisting of calcium carbonate (mainly in the form of aragonite crystals; Dannevig, 1956; Blacker, 1969; Bingel, 1981).

The complete annual growth zones of the otoliths are composed of one opaque and one hyaline zone. The age determinations are summarized to age-length keys regarding the first day of January as the date of birth. The age length keys are not seperated in sexes due to their negligible differences in growth (Hansen, 1949; Arnold, 1983). The calculations of the strength of the year classes as well as the estimates of the migration rates are based on the otolith material and length-frequencies obtained from the groundfish surveys only.

The morphology of the otoliths of the teleosts is species specific and used for taxonomical studies (Gaemers, 1976). In the fisheries biology the application of the morphometry (Marr, 1955) extends to the field of intraspecific differentiation (stock identification) although the phenotypical characteristics can be modified by the environmental conditions. On this account the second otolith of the individuals are measured after cleaning in water and drying 12 hours at 100°C. The length and the width of the otolith is measured to the tenth of a millimetre below using calipers. No attempt is made to correct the curvature. Templeman and Squires (1956) indicate an error of less than 0.1 mm concerning these measurements. The drying weight of the otolith is determined using a Satorius scale (2001 MP 2) calibrated in tenths of a milligram. The manufacturer of the scale defines a maximum variation of the weigths of 0.2 milligrams (fig. 7). Morphometric differences between the left and the right sagitta are not provable (Rojo, 1977). Therefore only one otolith is measured regardless which one of the two.

The Method of Otolith Typing

Describtion of the Method

The development of the method for the identification of the adolescent areas on individual basis by means of otolith typing is carried out by an international working group with the participation of scientists and technical assistants of the Institut für Seefischerei (Hamburg) and the Greenland Fisheries Research Institut (Copenhagen). Altogether 3 scientists and 4 technical assistants took part in the working group. During 5 meetings the method of the otolith typing is discussed, its application is improved and verified. On this occasion the common work is limited to the discussion and the slight modification of the describtion of typical annual growth zones in the cod otoliths proposed by the author and the evaluation of extensive otolith calssifications conducted by 5 otolith readers.

The author's field of activities covers the preparation of a collection of prototypes (otoliths, illustrations and photos) of distinct formations but also of transition types of annual growth zones in cod otoliths. The annual growth zones are described using the standard terminology for otolith readers established by Jensen (1963). Additionally the validation study of the method of otolith typing is carried out and presented to the working group by the author.

During the first meeting of the working group from the 29th of August till the 9th of September 1984 in Godthaab (Greenland) the structures of the cod otoliths are discussed regardless of the origin of the specimens (East or West Greenland). This resulted in a detailed definition and describtion of different types of annual growth zones in the otoliths prepared during the second meeting from the 6th till the 13th of March 1985 in Bremerhaven. The 3 types A, B and C are distinguished and described (s. Tab. 2).

The method for the identification of the adolescent areas of the cod is based on the typing of the annual growth zones in their otoliths. Each of the single annual growth zone is classified to one of the 3 types and recorded. The A-type indicates a pronounced regular growth whereas the B-type is characterized of an irregular growth producing no sharp but more diffuse demarcations between the opaque and the hyaline material. Annual growth zones of type C are bad identifiable and raise difficulties even to experienced otolith readers concerning the age determination. The central and marginal regions of the cod otoliths are describable separately using the classification of the single annual growth zones.

The A- and B-type, the most frequent types of annual growth zones, are shown in fig. 8 and 9. The opaque zones are white, and the hyaline zones are black in these illustrations. This manner of representation corresponds not with the brightness of the zones under the binocular microscope using transmitted light, but the difference in the light intensity of the zones is pointed out very clear with this colouration in the black and white drawings. The C-type of annual growth zones is not representable due to its extreme diffuse character.

Standardization of the Method

In the first instance the preparation and examination of the otoliths are standardized in order to obtain a good agreement in typing annual growth zones. The working group agreed on typing sawed otoliths only instead of broken otoliths. Additionally the side illumination of the otolith had the adventage over the practice of reflected light.

The porpose of the third and fourth meeting from the 2nd till the 6th of September 1985 (Copenhagen) and from the 14th till the 18th of April 1986 (Hamburg) was to improve the agreement in typing annual growth zones on the technical level using the collection of prototypes and comparing the numerous classifications of 5 otolith readers. So a general agreement of 80 % is achieved during the fourth meeting at which every otolith reader typified 1062 annual growth zones in 230 otoliths. This resulted in a slightly better agreement in typing the otoliths of the cod caught at West Greenland (s. Tab. 3). The working group considered this outcome, an error of less than 20 %, reproducible and adaequate for a validation study to verify the usability of the types of annual growth zones as natural tags and the identification of the adolescent areas.

Validation Study of the Method

The analysis of the geographic distribution pattern of the typical annual growth zones A, B and C is in the foreground regarding the valuation of the usability of the method. On this account fig. 10 shows the occurrence of the types of annual growth zones . The age groups from 1 to 9 of the years 1984, 1985 an 1986 are combined and the presence of the types is calculated (in per cent) for each annual growth zone.

From Fig. 10 it's visible that cod off West Greenland present clear and distinct structures in their otoliths. The A-Type is dominant in each age group and each annual growth zone. The diffuse B-types of annual growth zones are seldom and laid down mainly in the early periods of life, particularly at the age between 2 and 4 years. Annual growth zones of type C are practically not existent in the otoliths of cod caught in West Greenland waters.

The types of annual growth zones of the cod otoliths off East Greenland have a different distribution pattern compared to West Greenland (s. fig. 10). Up to the age of 5 years the B- and C-types are dominant, A-types occur rarely. But the A-types of annual growth zones gain in significance and displace the B- and C-types concerning the older age groups. The annual growth zones of type C show the trend to be more frequent at the edge of the otolith, accordingly in the bars in the rear of fig. 10.

The difference between West and East Greenland concerning the dominance of the types of annual growth zones in the cod otoliths up to the age of 5 years illustrates the usability of the otolith structures for the identification of the adolescent areas. The individuals get in their first years of life a visual natural tag by growing up in the West or East Greenland waters combined with the formation of A- or B- and C-types in the otoliths. Whereas the dominance of A-types in the otoliths of cod caught in West Greenland waters is unbiased by the age, the otolith structures of the cod off East Greenland change with increasing age from type B and C to type A. This relative increase of A-types of annual growth zones is explainable only by the immigration of cod off West Greenland older than 5 years, since the change of the dominance of the zone types even includes the annual growth zones of the first 5 years of life. In this early period of life the cod off East Greenland form only B- or C-types in their otoliths (s. fig. 10).

The similarities between 28 otolith samples selected at random are calculated in order to reconsider the information derived from the geographic distribution pattern of the annual growth zones by means of a method for numerical classification. All the samples from East and West Greenland considered in the similarity calculation include the otoliths of at least 30 specimens about the age of 5 years and younger. Only the numbers of A-, B- and C-types in the otoliths of these immature individuals are entered into the calculation of the similarities as characteristics of the otolith samples. The calculation of the similarities is carried out using the coefficient called "percentage similarity" (Whittaker and Fairbanks, 1958). The computations resulted in a matrix of similarity values. The similarity values are classified by means of a hierachical strategy (cluster analysis, average linkage method). Detailed describtions of the method for numerical classification are under consideration by Sneath and Sokal (1973) and Opitz (1980).

The similarity dendrogram classifies the otolith samples into two clusters or groups (s. fig. 11). The otolith samples off West Greenland belong exclusively to cluster 1 independent of the year of sampling, while cluster 2 consists only of otolith samples off East Greenland. The numerical classification of the origin of the otolith samples based on the formation of the annual growth zones of the individuals up to the age of 5 years confirms the usability of the otolith structures as a natural tag.

Formulation of an Algorithm for the Identification of the Adolescent Areas East and West Greenland on Individual Basis

The most certain information about the adolescent area of the cod off Greenland is derivable from the central region of the otoliths, since in this place the geographic distribution pattern of the types of annual growth zones is particularly different. Consequently it's meaningful to take only the formation of the first 5 annuli under consideraton as a criterion for the identification of the adolescent area. Each of the complete annual growth zone should be due to the same notice. So the normalization with the age of the specimen could enable the comparison with the other age groups.

The calculation of the dominance of the A-types among the first 5 annual growth zones is on offer because of their lack in the otoliths of juvenile cod off East Greenland. The mathematical function for the computation of the dominance of the A-types reads:

$$(15) \qquad F(x) = \sum_{i=1}^{AGE_{(max.\ 5)}} AGZ(A)_i * 100 \;/\; AGE_{(max.\ 5)}$$

with

$AGZ(A)_i$=annual growth zone of type A

AGE =age of the specimen in years

If the calculated value F(x) amounts to 50 or more the number of A-types is equivalent to the number of the other types of annual growth zones or the number of A-types is dominant. In this case the central region of the otolith is clear and distinct, an obvious indication for the adolescent area West Greenland. On the contrary the B- and C-types are dominant among the first 5 annual growth zones if the value F(x) amounts to less than 50. Individuals distinguished by diffuse central regions in their otoliths originate in all probability from East Greenland waters since they are almost lacking in the samples from West Greenland.

The dominance values of the A-types of the immature cod up to the age of 5 years from 1984, 1985 and 1986 are calculated in order to assess the error of the identification of the adolescent area. The information derived from the dominance values offers the calculation of the number of individuals which are related correctly in comparison with their actual catch positions. The numbers per age group of immature cod related correctly to their catch positions by means of the algorithm are entered in tab. 4. Regarding the otoliths of cod off West Greenland the correct identification of the adolescent areas on individual basis amounts from 70 to 75 %, while the identification for the individuals off East Greenland amounts to 90 % and is even better.

Also the error of the otolith typing itself amounts to 20 % and is not affected by the utilization of the algorithm. So the method described enables the identification of the adolescent areas of East or West Greenland with an error of 20 % on individual basis. This procedure meet the requirements to assess the migration of single year classes of the cod stocks off East and West Greenland following the valuation of the working group on typing cod otoliths.

The Cause of the Different Annual Growth Zones in Cod Otoliths

Wether the formation of the different annual growth zones is genetically determined or it is modified by the environmental conditions has to be viewed with concern by means of morphometric dimensions (fish length, otolith length, otolith width, otolith weigth). The morphological character of a specimen enables often valuable conclusions concerning genetically determined differences in comparison with specimens of the same species. For that reason the morphometry is an important criterion for the separation of stocks.

In the following the fish length and morphometric parameters of the otoliths are compared of those individuals distinguished by dominant A-types among the first 5 annual growth zones in their otoliths and those individuals characterized of dominant B- and C-types. The analysis is based on arithmetic averages since the numbers of morphometric measurements differ over the measuring range.

The functions of the following dimensions are calculated and put to the test on linearity (Sachs, 1984) :

	dependend variable	independend variable
A	otolith length	fish length
B	otolith width	fish length
C	otolith weight	fish length
D	otolith width	otolith length
E	otolith weight	otolith length
F	otolith weight	otolith width

The hypothesis of the test on linearity says that the function of the values is linear ($F_{tab.} \geq F_{cal.}$). Tab. 5 gives the values of the upper significance limits of the F-distribution and the calculated F-values. Additionally the type of the functions and the coefficients of correlation can be taken from tab. 5. The hypothesis of the test is not maintainable concerning the functions of the relative growth. All of them are characterized of high significant differences from the linearity (significance level of 0.001). The examined relations are fitted on exponential functions of the type $F(x) = ax^b$ with the exception of the relation D otolith width/otolith length, which is fitted on the sigmoid function of the type $F(x) = a/(1+be^{cx})$.

The regressions of the relative growth functions of those individuals distinguished by dominant A-types among the first 5 annual growth zones in their otoliths and those individuals characterized of dominant B- and C-types are put to the test of covariance in order to prove statistic differences between them. The test of covariance says that no statistic difference exists between the coefficients of regression ($t_{tab.} \geq t_{cal.}$). Tab. 6 gives the coefficients of regression and the limits of significance taken from the STUDENT-distribution as well as the calculated t-values. Statistic differences between the coefficients of regressions are not provable since the hypothesis of the test is not refutable on the significance level of 0.05.

Specimens with distinct and clear central regions or diffuse annual growth zones in their otoliths show no definable differences concerning the proportions examined. An indication of a genetically determined formation of the different annual growth zones in the otoliths of cod off Greenland is not provable. So the regressions are calculated again based on the total material without the separation into types. These recalculated regressions are available to the comparision with the other cod stocks of the North Atlantic Ocean (s. tab. 5 and fig. 12).

On the other hand a correlation between the formation of the different annual growth zones and the growth per unit of time seems evident. Fig. 13 illustrates the regressions between the average fish lengths per age group in relation to the numbers of A-zones (A) and the numbers of B-zones (B) in the otoliths. The correlations and regressions shown in fig. 13 are significant (significance level of 0.05).

From part A of fig. 13 it is obvious that the average lengths per age group decrease with increasing numbers of A-types of annual growth zones in the otoliths. On the contrary the individuals at the age of 4 to 7 years are characterized of increasing average fish lengths with increasing numbers of B-types in the otoliths (fig. 13, part B). These findings are valid for the otolith length, otolith width and otolith weight too, because the morphometric parameters are correlated significantly with the fish length. Definable results are not derivable from this examination concerning the C-types of annual growth zones due to their rare occurrence. The growth analysis indicates that fast growing specimens form B-types of annual growth zones in their otoliths whereas the slowly growing individuals form A-types. Consequently the otolith readers assess the growth conditions of the cod when typing the annual growth zones. The growth conditions, however are subject to a modification by changeable environmental conditions.

Application of the Method for the Identification of the Adolescent Areas and the Recalculation of the Population Dynamics

The method of otolith typing results in instantaneous informations about the origin and the migratory behaviour of the cod off Greenland. The population dynamics of the cod stocks off East and West Greenland are calculated without the emigration and the immigration (first part of the assessment tab. 7, 8, 9, 10) and under consideration of the migration rates in order to specify the effects of the migration. For all that the immigrants are regarded as an autonomous unit within the exploited stock and their population dynamics are calculated seperately from the population dynamics of the individuals grown up in the stock (second and third part of the assessment tab. 7, 8, 9, 10).

Immigration and Emigration of the Cod Stock off East Greenland

The chronological process within the cod stock off East Greenland from October 1984 till October 1986 is illustrated in fig. 14 and the assessment tab. 7 and 8. Not only the strength of the year classes from 1973 to 1985 are given but also their immigrated component derived from the otolith typing. The blank bars in fig. 14 give the total strength of the cohorts whereas the dotted bars specify the respective number of individuals immigrated from the stock off West Greenland. The illustrated values are entered in tab. 7 and 8.

First of all the outstanding increase of the recruiting cohorts 1984 and 1985 is remarkable, while the year classes 1982 and 1983 are very poor in individuals (fig. 14). Mainly this explosive development of the cohorts 1984 and 1985 accounts for the increase of the calculated stock abundance from 5,553,000 individuals in October 1984 to 17,686,000 in October 1986 (tab. 7 and 8). During the period of investigation the cohorts 1980 and 1981 are in their recruiting phase. So their strengths varying from 416,000 to 1,864,000 individuals assimilate to the abundance of the fully recruited year classes 1977, 1978 and 1979. During the period of investigation the cohorts 1980 up to 1985 are not fully recruited and they are not caught representatively. Nevertheless, from fig. 14 it's visible that the recruiting cohorts do not include remarkable parts of immigrants, since the respective dotted bars are very low or lacking. A considerable immigration into the cod stock off East Greenland is not provable regarding the juvenile individuals up to the age of 5 years.

On the other hand the fully recruited cohorts 1973-79 include immigrants from West Greenland (dotted bars in fig. 14). Here only the dominant year classes 1977 and 1979 are described, since the cohorts 1973-76 are very poor in individuals. The blank bars of the year class 1979 show an increase in the total number of individuals over the period from 1984 till 1986. But the respective dotted bars representing the immigrants become longer too and point out that the increase of the total number of individuals is due to an immigration of cod from West Greenland. In October 1984 the number of immigrants of the year class 1979 amounts to 311,000 individuals while in October 1986 the number of immigrants of the same cohort amounts to 843,000 (tab. 7 and 8). During the period of investigation a strong immigration happened for the first time within the year class 1979 at the age of 5 to 7 years. The instantanous immigration of individuals of the cohort 1979 from West Greenland into the stock off East Greenalnd amounts to 536,000 from October 1984 till October 1985 and to 505,000 from October 1985 till October 1986.

Also the year class 1977 include large numbers of immigrants (dotted bars in fig. 14). In the first year of investigation the total number of individuals increases from 1,630,000 to 1,752,000 and decreases to 1,250,000 in the year after. In the first year the number of immigrants increases too and causes a strong instantanous immigration of 847,000 individuals. During the second period from October 1985 till October 1986 the number of individuals immigrated from West Greenland decreases from 1,373,000 to 943,000. This loss of immigrants is due to the fishing mortality and the natural mortality as well as the emigration to Iceland, which is ignored by the calculation model. Consequently, no further immigration from West Greenland happened during the second period concerning the year class 1977.

The cod at the age from 5 to 8 years show a pronounced migratory behaviour from West to East Greenland, while a migration of the older individuals is not provable due to their very low year class strengths. The continous immigration of the cod at the age from 5 to 8 years results in the increase of the relative components of the immigrants within the single year classes. At the beginning of the investigation in October 1984 the relative component of the immigrants of the year class 1979 amounts to 35 % and increases to 75 % in the cohort 1977 at the end.

The high and negative Z_{N+I}-values of the fully recruited cohorts 1977 and 1979 demonstrate the motivation for the planning and the realization of this project. Negative values of the total mortality are not expected concerning fully recruited year classes in an exploited stock, their total mortalities should be positive. The negative Z_{N+I}-values are the result of the strong and fast immigration from West Greenland. In the most cases the Z_N-values of the cod grown up in the stock off East Greenland are higher campared to the Z_{N+I}-values since here the effect of the immigration is avoided (tab. 7 and 8).

The numbers of individuals emigrated to West Greenland are entered into the column E'_N of the tab. 7 and 8. The values of the fully recruited cohorts are negative and put in brackets, since no positive emigration happened and they represent the returning emigrants. For that reason the coefficients of emigrants of the fully recruited cohorts are 0. Only the recruiting cohorts show positive numbers of emigrants, but their individuals are not caught representatively. However, these values make an emigration of immature cod from East to West Greenland evident.

Immigration and Emigration of the Cod Stock off West Greenland

The dynamic of the year classes 1973-85 of the cod stock off West Greenland is illustrated in fig. 15 and the assessment tab. 9 and 10. As has been said above the blank bars in fig. 15 give the total strength of the year classes whereas the dotted bars represent the respective number of immigrants originating from East Greenland in this case. Again the illustrated values are listed in the assessment tab. 9 and 10 seperated into the two periods from November 1984 till November 1985 and from November 1985 till November 1986.

In November 1984 the 0-group is caught for the first time by the groundfish survey (fig. 15). In November 1985 cod of the year class 1985 are found too. The fig. 15 is not able to show the explosive development of the cohorts 1984 and 1985, since the number of individuals overtop widely the chosen scale of the illustration. The long dotted bars demonstrate that during the period of investigation the cohorts 1984 and 1985 include considerable components of individuals immigrated from East Greenland. The year classes 1982 and 1983 are very poor in individuals compared to the cohorts 1984 and 1985. From 1984 till 1985 the year class 1980 and the more abundant cohort 1981 are in their recruiting phase, since their numbers of individuals are still increasing. The components of immigrants of the year classes 1980-83 are negligible in comparison with the numbers of individuals grown up within the cod stock off West Greenland. In no case the immature individuals of the cohorts 1980-85 are fully recruited into the exploited stock and their numbers are not comparable to the older year classes. As the cod stock of East Greenland the stock off West Greenland increases in abundance from 16,106,000 individuals in November 1984 to 134,717,000 in November 1986 due to the occurrence of the recruiting cohorts 1984 and 1985 (tab. 9 and 10).

During the period of investigation the year class 1979 was dominant among the cohorts which are caught representatively. But the total numbers of individuals of this cohort decreases drastically from 9,120,000 in November 1984 to 3,441,000 in November 1986. The respective numbers of immigrants are unimportant and decrease in addition (dotted bars in fig. 15). The chronological developments of the year class 1977 and 1979 are directly comparable whereas the cohort 1978 is to poor in individuals. Also the numbers of individuals of the year class 1977 decrease from 1,991,000 to 403,000. Additionally the immigrants of this cohort originating from East Greenland reduce very much. The process of the remaining cohorts 1973-76 is not describable since they are very poor in individuals.

During the period of investigation remarkable immigrations are only provable within the recruiting cohorts 1980-85 (tab. 9 and 10). Here the relative components of the immigrants amount from 15 % to 38 %. But also these values of the non-fully recruited year classes merely demonstrate that a migration of immature cod from East to West Greenland happens. The cod at the age up to 4 years are not caught representatively and therefore this immigration is not assessable. The fully recruited cohorts 1973-79 include only very few immigrants and their numbers decrease strongly from November 1984 till November 1986. Consequently, an instantaneous immigration is not evident concerning the year classes 1973-79. The values of the instantaneous immigration I' are negative and put in brackets in order to demonstrate that no positive immigration exists (tab. 9 and 10).

The very low numbers of individuals of the age groups >7 years in addition to the drastically decrease of the abundance of the dominant year classes 1977 and 1979 during the time from November 1984 till November 1986 point to extreme high losses of individuals (fig. 15). Actually the values of the mortality Z_{N+I} of the total year class strengths are much higher compared to the Z_{N+I}-values of the cod stock off East Greenland regarding the fully recruited cohorts only (tab. 7, 8, 9, 10). That accounts for a strong emigration since such high losses of individuals are not explainable by fishing and natural mortalities.

The numbers of emigrants per year class are entered into the column E'_N of tab. 9 and 10. From November 1984 till November 1985 the cohorts 1977 and 1979 show considerable numbers of emigrants mounting to 847,000 and 536,000 individuals respectively (tab.9). This strong emigration causes high coefficients of emigration E_N reaching their maximum level at 0.65. One year after only the cohort 1979 present a remarkable number of emigrants. From November 1985 till November 1986 505,000 individuals of the cohort 1979 left the cod stock off West Greenland (tab. 10). As in the first part of the period of investigation the coefficients of emigration E_N firstly are increasing with age to a maximum value and thereafter decreasing to 0 in the second part too. The individuals start the emigration at the age of 5 years reaching the peak at the age of 7 years while an emigration of the older specimens is not provable due to their negligible numbers.

Discussion

Discussion of the Method of Otolith Typing

At all times the examination of the migratory behaviour of fish is of great importance in fisheries biology, because the stock assessments can be affected with unknown emigration and immigration rates. Tagging experiments impart knowledge of the migration of fish. Unfortunately the recoveries of tagged specimens are very rare and they inform about the main direction and the distance covered only. But an assessment of the migration rates is impracticable in principle by means of tagging.

The biologists endeavour to read from the scales and otoliths some additional informations about the sexual development of the individuals, their growth of former periods of life and their belonging to stocks. Rollefsen (1934, 1935) uses the otoliths of cod off Norway not only to determine the time of maturation but also to separate between stocks by means of typical zone formations in the otoliths. In doing this Rollefsen identifies a natural tag and recognizes the migrations of the cod. Einharsson (1949) is able to discriminate spring spawning herring from autumn spawning herring by means of otolith types, a procedure which is confirmed by Parrish and Sharman (1959) concerning the North Sea and Messieh (1972) concerning the costal area off Newfoundland. Gaemers (1976) demonstrates the evolution of the Gadidae based on otolith investigations. Increasingly even quantitative results on fish migrations are derivable since natural tags yield much more informations than tagging experiments (Rauck, 1973).

The majority of the describtions of natural tags in cod otoliths available in the literature can be devided into 2 groups. The first group is distinguished from the second by the subjective typings of noticable characteristics. Rollefsen (1933) describes the occurrence of narrow and broad growth zones in the otoliths, which are adopted by Godo (1984) in order to separate stocks. Bingel (1972) classifies 5 types of otoliths based on the formation of the first annual growth zone only while Berner (1968) subdivides the otoliths into easy determinable otoliths, into difficult determinable otoliths and into non-determinable otoliths. On the contrary the natural tag used by Trout (1954) belongs to the latter group of otolith typings, which is characterized of the measurements of the annual growth zones. He measures *not only* the dimensions of the first and second annual growth zones like most of the authors do (L1- and L2-measurements), but he also derives the growth pattern of the individuals from the measurements of all annual growth zones. Thereafter the growth pattern is used as a criterion of the stocks.

By comparison of the 2 groups of natural tags the latter seems to be the more reliable because this group is based on measurements in contrast to subjective characteristics. However, clear definable measurements do not exist in an otolith looked at more closely. The measurements of the annual growth increments are subject to the personal valuation regarding the diffuse otoliths in particular. As well the measurements of the annual growth zones are not reproducible but a subjective criterion.

In this investigation the application of the formation of the annual growth zones in the otoliths as a natural tag is postulated. The single annual growth zones are classified to 3 different types (A, B and C). The 3 types of annual growth zones are documented by detailed describtions (tab. 2) and illustrations (fig. 8,and 9). The typing of the annual growth zones carried out in parallel to the age determination results in informations about their structures which can be analyzed quickly. The analysis considers separately the central and the marginal region of the otoliths. From the beginning the examination of the natural tag was limited to the otoliths of the cod off Greenland, since some practical knowledge of the typing of cod otoliths is described in the literature already and the experienced otolith readers kept on pointing on distinct zone formations.

The percentage agreement in typing of the annual growth zones between 5 otolith readers is improved and amounts to 80 % (tab. 3). An additional reduction of the misclassification amounting to 20 % is hardly to achieve, because the typing of the annual growth zones is based on personal valuations after all, in spite of the detailed describtions and collections of prototypes.

Each kind of natural tags used for the determination of the origin necessitates a study of validation. This requirement meets the distinct distribution pattern of the 3 different types of annual growth zones. The A-type dominates in the otoliths of cod off West Greeland, whereas during the first 5 years of life the individuals off East Greenland form predominantly B- and C-types in their otoliths (fig. 10). The relation of the individuals to their adolescent areas is carried out using an algorithm, which computes the dominance of the A-types among the first 5 annual growth zones in the otolith. The conclusion drawn from the algorithm concerning the adolescent area of an individual is limited to its favourite adolescent area during the early life period, since the algorithm takes into accout merely the presence of the A-types but not the sequence. The comparison between the probable adolescent area derived from the algorithm and the real catch positions of juvenile individuals (age <6 years) demonstrates the practicability of the identification of the adolescent areas East and West Greenland with an error of 20 % on individual basis (tab. 4).

During the time of investigation from 1984 till 1986 about 13,000 identifications of the adolescent area are carried out based of the formation of the annual growth zones in the cod otoliths. The examination of a large number of otoliths is required, since the information about the numbers of immigrants is obtained from the age-length key in addition to the age composition of the stock. In this study it is aimed to collect the otoliths of at least 30 specimens per length class (3 cm). In fact the most frequent length classes contain the multiple of 30 pairs of otoliths.

The tagging experiments demonstrate that the cod stocks of the North Atlantic Ocean are connected by means of long-distance migrations of single individuals (Gulland and Williamson, 1962; Cushing, 1985). Consequently, the genetic distance between the sympatric cod stocks is negligible, only the cod stock in the

Baltic is identifiable (Mork et al., 1985). Lühmann (1954) describes the otoliths of the Baltic cod as dumpy and more compact in comparison with the elongated and more slender otoliths of the cod off Iceland.

The analysis of the morphometry of the otoliths gives no indication of a genetically determined formation of the different annual growth zones in accordance with the negligible genetic variation of the Atlantic Cod (tab. 6). In contrast the validation study points to the presumption that the formation of the different annual growth zones is due to the growth of the individuals (fig. 13). Bingel (1977) proves the effects of variations in temperature, salinity, oxygen and food on the character of the zone structures in the otoliths. The formation of opaque and hyaline zones is affected by the seasonal changes in concentrations of protein and calcium of the endolymph (Mugiya, 1964 and 1966) flowing around the otolith in the labyrinthine organ (Dale, 1976).

The hydrographic conditions of the West Greenland waters slow down the growth of the cod since here the positive influence of the warmer water is limited to a short period (Taylor, 1958). The maximum input of heat by the Irminger Current happens from October till December. The dominant low temperature combined with short seasonal warmings causes the clear and distinct opaque and hyaline growth zones, which are classified to type A (fig. 8).

On the other hand the growth of the cod off East Greenland is faster due to the twelve-month influence of the warm Atlantic water (Irminger Current). Stein (1987 a) descrbes a great instability of the meandering water masses off East Greenland. So during the time of 2 days variations of 5 °C are possible in the bottom layer. The dominant warm temperature combined with short-time coolings causes the faster growth and the formation of B- and C-types (fig. 9). In all probability the short-time variations in temperature affect the formation of the numerous check rings.

The hydrographic conditions off East and West Greenland are manifested in the otoliths of the poikilotherm fishes in the fdrm of different annual growth zones. The different annual growth zones used as a natural tag offer the identification of the adolescent area on individual basis. The personal valuation of the different annual growth zones and their modification by changeable environmental parameters require a permanent control of the typing by a responsible scientist. This is essential, since the short period of 3 years gives to this investigation only the character of a pilot study. Therefore the applicability of the method of otolith typing has to be reconsidered every year, because unusual variations in water temperature will cause different annual growth zones. The result of the cluster analysis of otolith samples demostrates the constant formation of types of annual growth zones during the period of investigation from 1984 till 1986 (fig. 11).

Further investigations should not concentrate exclusively upon the microstructures of the growth zones. Though Irie (1960) shows that the aragonite cristals are smaller in the opaque zones and therefore bias the transparency in comparison with the hyaline zones. The existence of daily growth layers described by Panella (1973) is not directly confirmed by Steffensen (1980), since the dates of birth determined by means of counting the fine ring structures do not correspond always with the known time of the larval hatch. The differences in time are explained by the long continous spawning season and very narrow daily layers, which are not distinguishable by means of a microscope (200 x magnification).

The derivation of the water temperature from the isotope-fractions should be more promising as pointed out by Degens et al. (1969) and Radtke (1984). Wefer (1985) gives positive correlations between the oxygen isotope ^{18}O and the isotope of carbon ^{13}C, while Devereux (1967) analyzes the rations of the oxygen isotope ^{16}O and ^{18}O in the otoliths only. The migratory behaviour of the cod off Greenland should be describable by means of the measurements of the fractions of stable isotopes too, since the hydrographic conditions of the nursery grounds off East and West Greenland are different.

Discussion of the Application of the Method for the Identification of the Adolescent Areas and the Recalculation of the Population Dynamics

The migration of the cod off Greenland is classified to a long-distance oceanodromous migration following the definitions of McKeown (1984). He distinguishes the passive and active changes in locality into 4 categories with different importance concerning the ecology and evolution. Fishes migrate in order to optimize their food intake, to avoid unfavourable environmental conditions, to reproduce and in order to expand their distribution by means of colonization.

First of all it is necessary to make mention of the restrictions, which are determined by the sampling and the calculation model of the emigration and immigration before discussing the results of the application of the method. So the fishing is limited from 6 o'clock a. m. till 8 o'clock p. m. Therefore it is renounced to examine the diurnal factors. But also the important seasonal changes are not analyzed, since the groundfish survey is carried out yearly in autumn. Here the periodic migration from the banks to the fjord area is remarkable as described by Jean (1964) and Templeman (1974) regarding the cod stock off Newfoundland. Even the question about the seasonal changes in intensity of the migration is not answerable on the basis of the data collected. The strategy of the otolith sampling is length-stratified. Consequently, an examination of the regional occurrence of the 3 types of annual growth zones is not practicable.

The fjord area of Greenland is not covered by the survey, because the ground is unsuitable for a bottom trawl. On this account Hovgard et al. (1988) established a new longline survey covering both the offshore area and the fjord area. They find, that in autumn the part of the cod stock living in the fjord area amounts to 25 % of the calculated stock abundance. Additionally to the fjord component, which is not directly determinable, the high variability of the abundance values complicates the stock assessment. Ehrich (1987) demonstrates by means of a comparative fishing experiment that the variabilities of the catches of some fish species decrease within reduced survey areas. The confidence limits of the calculated stock abundance should be reducible with the concentration of the practicable hauls on smaller parts of the survey area. Sahrhage (1980) and Messtorff (1980) refer to the depth-related occurrence of cod already. However, the values of abundance as well as the emigration and immigration rates derived from the groundfish survey should be considered to be indices and not absolute values.

The calculation model of the emigration and the immigration takes into account the cod stocks off East and West Greenland but not the emigration of adult individuals to Iceland (fig. 1). This restiction represent the most important difference between the calculation model and the reality. Jones (1978) determined the emigration rate to Iceland by means of a modified virtual population analysis and the theoretical coefficient of emigration 0.2. Easey (1978) uses otolith typings in order to assess the immigrated component of the Icelandic cod stock originating from Greenland. Nevertheless, he points to the fact, that the typical Greenlandic otoliths could be formed as well by individuals of the Icelandic stock under the same hydrographic conditions. To quantify the immigrants of the cod stock off Iceland a more precise validation is required. An additional restriction consists in the exclusion of the returing emigrants, because the algorithm for the identification of the adolescent area is not able to identify always those individuals, which emigrated first and returned afterwards.

The assessment of the migration based on the method of otolith typing confirms the idea of the migratory behaviour of the cod off

Greenland derived from tagging experiments (Meyer, 1965 a). An emigration of adult individuals from the cod stock off East to West Greenland is not provable. During the period of investigation a lost of individuals in this direction is noticed regarding the juvenile cod. This emigration of specimens of the non-fully recruited cohorts is not assessable, because they are not caught representatively by the groundfish survey. The immigration into the cod stock off East Greenland starts with individuals at the age of 5 years and the immigrants contribute as many as 75 % of the total strength of the older year classes (fig. 14). The very low total mortalities of the fully recruited cohorts are explainable only by the separation of the stock into the individuals grown up within the exploited stock and the increasing immigrated component (tab. 7 and 8).

On the other hand remarkable numbers of immigrants are provable only within the non-fully recruited cohorts regarding the cod stock off West Greenland (fig. 15). As above the calculated abundances of the juvenile cod are not comparable to the values of the fully recruited cohorts. Losses of individuals of the non-fully recruited cohorts due to the emigration are not observed concerning the cod stock off West Greenland. Against it the coefficients of emigration of the fully recruited year classes are calculated directly. The coefficients of emigration increase with increasing age to a maximum of 0.65 and represent a strong emigration to East Greenland. This calculated emigration causes the very high values of total mortalities of the fully recruited cohorts (tab.9 and 10). Unfortunately the fishing mortalities of the recruiting cohorts are very high. Consequently, quantitative results are not derivable concerning the older age groups (>8 years). The concentration of the fishery on the juvenile cod under 5 years of age is not detected at the beginning of the 1970-79 decade (Schumacher, 1971).

The results of this investigation are of some importance concerning the stock assessment and the catch prediction. In particular an improvement is obtainable with the consideration of the increasing emigration of the cod off West Greenland with increasing age in contrast to the constant emigration and immigration rates used by the international working groups of the ICES and NAFO. This requires the application of the method of otolith typing in order to separate the exploited stock into the individuals grown up within the stock and the immigrants. The separated and direct assessment of the immigration of cod originating from West Greenland into the cod stock off East Greenland offers an improvement in the advice of the fisheries management regarding the catch predictions of both stocks.

The described migration of the cod off Greenland corresponds with the general concept of the migratory behaviour of fish developed by Harden Jones (1968). It consists of a passive larval drift following the current to the nursery grounds and an active motion of the adults back to the spawning grounds against the current (fig. 1). The presumption is obvious, that the migration of the cod off Greenland beginning at the age of 5 years is a matter of the homing phenomenon. This phenomenon designates the impulse of the movement back to the location of the own origin, which is characteristic of a lot of fish species. The mechanism of orientation seems to be due to a positive rheotaxis.

Only a longer period of investigation in addition to seasonal examinations offers a more detailed analysis of the factors affecting the migration. Most likely one of these factors is the maturation of the gonads, since the migration of the individuals starts at the age of 5 years and the coefficient of emigration increases with increasing age. The intensity of the migration is determined mainly by the strength of the cohorts. Open questions are wether a food competition or although a possible mutual stimulation affects positive the emigration of the cohorts, which are rich in individuals. Certainly the water temperature is one more factor exercising an influence on the migration of the cod off Greenland. This investigation is carried out during a pronounced warm period (Messtorff and Stein, 1988). As a migration factor the variability of the temperature is of great importance, since the cod off Greenland live at their northerly limitation.

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Tab. 1 Material of otoliths. Time of otolith sampling and numbers of otoliths (+ = commercial trawlers)

Vessel	East Greenland Time	Number of otoliths	West Greenland Time	Number of otoliths
MS Wesermünde+	17.09.-06.10.84	485	27.09.-01.10.84	257
MS Hannover+			28.09.-30.09.84	103
FB Anton Dohrn	15.10.-23.10.84	384	25.10.-18.11.84	2,418
MS Hannover+	18.03.-27.03.85	648	28.02.-16.03.85	874
FFB Walther Herwig	01.10.-02.11.85	1,881	19.11.-11.12.85	2,577
MS Hannover+	19.03.-23.03.86	270	11.03.-11.03.86	199
MS Mainz+	30.03.-30.03.86	159		
FFB Walther Herwig	03.09.-02.10.86	1,383	13.10.-13.11.86	1,592

Tab. 2 Describtions of the 3 types of annual growth zones in cod otoliths.

Type A : The annual growth zone is divided into a compact opaque and a hyaline zone. The hyaline zone consists of either a compact ring or only few rings (brigth in transmitted light) laying closely together and clearly separated from the neighbouring opaque zones.

Type B : The opaque and hyaline components of the annual growth zones are not compact. The diffuse character originates from fine ring structures which form relatively broad transitional zones or secondary (check) rings. No sharp borders exist between the zones but they still form an easily seen system of annuli.

Type C : Some of the innermost annual growth zones are relatively easy to identify and could eventually be classified as type A or B, although the hyaline component seems to be of a slightly different nature, in some cases it has a middle opaque part giving the character of a hyaline double zone. Thereafter the otolith looses the clear separation between hyaline and opaque zones and changes to a different diffuse nature. Experienced readers, however might still be able to determine the age on the basis of unclear and shadowy structures.

Tab. 3 Percentage agreement in typing of 1062 annual growth zones in 230 cod otoliths between 5 otolith readers.

Identification number of the otolith reader	1	2	3	4	5
1		91	90	88	89
2	81		85	86	86
3	86	73		86	86
4	86	78	83		88
5	89	83	87	84	

cod otoliths East Greenland (below the diagonal)

cod otoliths West Greenland (above the diagonal)

Tab. 4 Examination of the algorithm for the identification of the adolescent areas. Percentage per age group of the individuals related correctly in comparison with their actual catch positions.

Age	West Greenland n	West Greenland %	East Greenland n	East Greenland %
1	899	70	488	92
2	707	76	736	96
3	529	73	212	98
4	810	85	520	89
5	1,897	84	645	91

Tab. 5 Cod off Greenland. Test on linearity and functions of relative growth.

MORPHOMETRIC DIMENSIONS DEPENDEND VARIABLE	INDEPENDEND VARIABLE		$F_{TAB.}$ (FGR., 0.001) TEST ON LINEARITY		$F_{CAL.}$	TYPE OF FUNCTION	FUNCTION	COEFFICIENT OF CORRELATION
A OTOLITH LENGTH (MM)	FISH LENGTH (CM)	A-TYPE DOMINANT	2.13	>	39.41	exponential	$F(x)=1.501x^{0.575}$	0.996
		B- AND C-TYPE DOMINANT	2.13	>	64.21	exponential	$F(x)=1.552x^{0.568}$	0.996
		TOTAL	2.13	>	63.43	exponential	$F(x)=1.526x^{0.572}$	0.996
B OTOLITH WIDTH (MM)	FISH LENGTH (CM)	A-TYPE DOMINANT	2.27	>	35.24	exponential	$F(x)=0.451x^{0.691}$	0.998
		B- AND C-TYPE DOMINANT	2.27	>	33.61	exponential	$F(x)=0.480x^{0.676}$	0.997
		TOTAL	2.27	>	65.72	exponential	$F(x)=0.461x^{0.685}$	0.998
C OTOLITH WEIGHT (MG)	FISH LENGTH (CM)	A-TYPE DOMINANT	2.27	>	52.69	exponential	$F(x)=0.116x^{1.968}$	0.999
		B- AND C-TYPE DOMINANT	2.27	>	16.23	exponential	$F(x)=0.117x^{1.960}$	0.998
		TOTAL	2.27	>	63.22	exponential	$F(x)=0.116x^{1.965}$	0.999
D OTOLITH WIDTH (MM)	OTOLITH LENGTH (MM)	A-TYPE DOMINANT	2.13	>	3.89	sigmoid	$F(x)=12.36/(1+10.535e^{-0.179x})$	0.999
		B- AND C-TYPE DOMINANT	2.13	>	3.75	sigmoid	$F(x)=12.46/(1+10.723e^{-0.179x})$	0.998
		TOTAL	2.13	>	6.65	sigmoid	$F(x)=12.36/(1+10.671e^{-0.179x})$	0.999
E OTOLITH WEIGHT (MG)	OTOLITH LENGTH (MM)	A-TYPE DOMINANT	2.13	>	98.10	exponential	$F(x)=0.053x^{3.184}$	0.999
		B- AND C-TYPE DOMINANT	2.13	>	48.54	exponential	$F(x)=0.043x^{3.257}$	0.999
		TOTAL	2.13	>	145.98	exponential	$F(x)=0.047x^{3.216}$	0.999
F OTOLITH WEIGHT (MG)	OTOLITH WIDTH (MM)	A-TYPE DOMINANT	2.74	>	263.94	exponential	$F(x)=1.251x^{2.787}$	0.999
		B- AND C-TYPE DOMINANT	2.74	>	121.11	exponential	$F(x)=1.136x^{2.327}$	0.999
		TOTAL	2.74	>	377.03	exponential	$F(x)=1.215x^{2.798}$	0.999

Tab. 6 Cod off Greenland. Coefficients of regression and test on covariance (significance level of 0.05).

morphometric dimensions	coefficients of regression A-type dominant	B- and C-type dominant	$t_{tab.}$	$t_{cal.}$
otolith length / fish length	0.575	0.568	2.012 ≥	0.482
otolith width / fish length	0.691	0.676	2.018 ≥	1.050
otolith weight / fish length	1.968	1.960	2.018 ≥	0.221
otolith width / otolith length	0.179	0.179	coeff. ident.	
otolith weight / otolith length	3.184	3.257	2.009 ≥	1.871
otolith weight / otolith width	2.787	2.827	2.056 ≥	1.052

Tab. 7 Cod stock off East Greenland. Assessment table from October 1984 till October 1985 (n x 1000).

	TOTAL			COD GROWN UP WITHIN THE EXPLOITED STOCK								IMMIGRATED COD						
YEAR CLASS	$N_{t1}+I_{t1}$	$N_{t2}+I_{t2}$	Z_{N+I}	N_{t1}	N_{t2}	F'_N	E'_N	Z_N	F_N	E_N	M_N	I_{t1}	I_{t2}	F'_I	F_I	M_I	Z_I	I'
1973	182	47	1.35	100	18	0	0	1.71	0	0	1.71	82	29	0	0	0.2	0.20	(-38)
1974	37	37	0	0	6	1	0	/	/	0	/	37	31	3	0.08	0.2	0.28	3
1975	128	61	0.74	10	19	4	(-4)	-0.64	0.51	0	-1.15	119	42	8	0.07	0.2	0.27	(-49)
1976	492	266	0.61	118	63	5	(-2)	0.55	0.04	0	0.51	373	198	14	0.04	0.2	0.24	(-95)
1977	1630	1752	-0.07	839	381	43	(-57)	0.79	0.05	0	0.74	792	1373	153	0.21	0.2	0.41	847
1978	704	674	0.04	459	370	58	(-1)	0.22	0.14	0	0.08	243	303	47	0.21	0.2	0.41	142
1979	896	1406	-0.45	586	716	123	(-589)	-0.20	0.24	0	-0.44	311	694	119	0.48	0.2	0.68	536
1980	416	1488	-1.27	396	1444	108	61	-1.29	0.32	0.32	-1.78	20	46	3	0.16	0.2	0.36	32
1981	982	1468	-0.40	973	1336	31	458	-0.32	0.03	0.64	-0.99	10	134	3	0.36	0.2	0.56	128
1982	70	61	0.14	70	55	/	96	-0.24	/	/	/	/	6	/	/	/	/	6
1983	16	285	-2.88	16	270	/	659	-2.83	/	/	/	/	14	/	/	/	/	14
1984	/	1106	/	/	940	/	11226	/	/	/	/	/	165	/	/	/	/	165
1985	/	214	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
Sum	5553	8865		3567	5623	373	12500					1987	3035	350				1873

For the elaboration of the table see page 7-12 !
Note: Differences in sums are due to rounding errors and the occurrence of the 0-group !

Legend :
- t1 -October 1984
- t2 -October 1985
- N_{t1} -number of cod grown up within the exploited stock at the time t1
- N_{t2} -number of cod grown up within the exploited stock at the time t2
- I_{t1} -number of cod immigrated at the time t1
- I_{t2} -number of cod immigrated at the time t2
- Z_{N+I} -total mortality of the cod grown up within the exploited stock and the immigrants
- Z_N -total mortality of the cod grown up within the exploited stock
- Z_I -total mortality of the immigrants
- F'_N -number of cod grown up within the exploited stock and died by fishery
- F_N -fishing mortality of the cod grown up within the exploited stock
- F'_I -number of cod immigrated and died by fishery
- F_I -fishing mortality of the cod immigrated
- E'_N -number of cod grown up within the exploited stock and emigrated
- E_N -instantaneous emigration of the cod grown up within the exploited stock
- M_N -natural mortality of the cod grown up within the exploited stock
- M_I -natural mortality of the cod immigrated
- I' -number of cod immigrated during time t1 and t2 (instantaneous immigration)

Tab. 8 Cod stock off East Greenland. Assessment table from October 1985 till October 1986 (n x 1000).

	TOTAL			COD GROWN UP WITHIN THE EXPLOITED STOCK								IMMIGRATED COD						
YEAR CLASS	$N_{t1}+I_{t1}$	$N_{t2}+I_{t2}$	Z_{N+I}	N_{t1}	N_{t2}	F'_N	E'_N	Z_N	F_N	E_N	M_N	I_{t1}	I_{t2}	F'_I	F_I	M_I	Z_I	I'
1973	47	71	-0.41	18	16	0	0	1.18	0	0	1.18	29	55	0	0	0.2	0.20	31
1974	37	9	1.41	6	0	0	0	/	0	0	/	31	9	0	0	0.2	0.20	(-16)
1975	61	83	-0.31	19	47	1	0	-0.91	0.05	0	-0.96	42	36	1	0.02	0.2	0.22	2
1976	266	88	1.11	68	18	1	(-2)	1.33	0.01	0	1.32	198	70	4	0.02	0.2	0.22	(-89)
1977	1752	1256	0.33	381	313	23	(-24)	0.20	0.06	0	0.14	1373	943	69	0.05	0.2	0.25	(-126)
1978	674	452	0.40	370	201	29	(-42)	0.61	0.08	0	0.53	303	252	35	0.12	0.2	0.32	32
1979	1406	1742	-0.21	716	899	300	(-71)	-0.23	0.54	0	-0.77	694	843	292	0.52	0.2	0.72	505
1980	1488	898	0.51	1444	867	248	(-121)	0.51	0.19	0	0.32	46	32	9	0.22	0.2	0.42	2
1981	1468	1864	-0.24	1336	1656	188	(-283)	-0.21	0.15	0	-0.36	134	181	20	0.16	0.2	0.36	88
1982	61	391	-1.86	55	391	45	213	-1.96	1.70	/	/	6	0	0	0	0.2	0.20	(-5)
1983	285	1584	-1.72	270	1569	56	1298	-1.76	0.23	/	/	14	15	1	0.07	0.2	0.27	4
1984	1106	5827	-1.66	940	5797	/	31359	-1.82	/	/	/	165	31	/	/	/	/	(-104)
1985	214	3451	-2.78	/	3416	/	1513	/	/	/	/	/	35	/	/	/	/	35
Sum	8865	17686		5623	15190	890	34383					3035	2502	421				699

For the elaboration of the table see page 7-12 !

Note: Differences in sums are due to rounding errors and the occurrence of the 0-group !

Legend :
- t1 -October 1985
- t2 -October 1986
- N_{t1} -number of cod grown up within the exploited stock at the time t1
- N_{t2} -number of cod grown up within the exploited stock at the time t2
- I_{t1} -number of cod immigrated at the time t1
- I_{t2} -number of cod immigrated at the time t2
- Z_{N+I} -total mortality of the cod grown up within the exploited stock and the immigrants
- Z_N -total mortality of the cod grown up within the exploited stock
- Z_I -total mortality of the immigrants
- F'_N -number of cod grown up within the exploited stock and died by fishery
- F_N -fishing mortality of the cod grown up within the exploited stock
- F'_I -number of cod immigrated and died by fishery
- F_I -fishing mortality of the cod immigrated
- E'_N -number of cod grown up within the exploited stock and emigrated
- E_N -instantaneous emigration of the cod grown up within the exploited stock
- M_N -natural mortality of the cod grown up within the exploited stock
- M_I -natural mortality of the cod immigrated
- I' -number of cod immigrated during time t1 and t2 (instantaneous immigration)

Tab. 9 Cod stock off West Greenland. Assessment table from November 1984 till November 1985 (n x 1000).

YEAR CLASS	TOTAL $N_{t1}+I_{t1}$	$N_{t2}+I_{t2}$	Z_{N+I}	COD GROWN UP WITHIN THE EXPLOITED STOCK N_{t1}	N_{t2}	F'_N	E'_N	Z_N	F_N	E_N	M_N	IMMIGRATED COD I_{t1}	I_{t2}	F'_I	F_I	M_I	Z_I	I'
1973	0	0	/	0	0	0	(-38)	/	0	0	/	0	0	0	/	/	/	0
1974	36	0	/	32	0	8	3	/	0.29	0.10	/	0	0	0	/	/	/	0
1975	216	20	2.38	211	20	13	(-49)	2.36	0.06	0	2.30	5	0	0	0	0.2	0.20	(-4)
1976	93	22	1.44	78	12	17	(-95)	1.87	0.25	0	1.62	15	10	15	/	0.2	0.20	(-2)
1977	1991	599	1.20	1772	540	698	847	1.19	0.50	0.65	0.04	221	60	78	0.44	0.2	0.64	(-57)
1978	822	345	0.87	651	265	234	142	0.90	0.45	0.25	0.20	168	79	70	0.54	0.2	0.74	(-1)
1979	9120	6342	0.36	7518	5933	5393	536	0.24	1.26	0.07	-1.09	1598	410	373	0.27	0.2	0.47	(-589)
1980	1483	2254	-0.42	1185	2025	1014	32	-0.54	1.94	0.03	-2.51	299	228	114	0.48	0.2	0.68	61
1981	2074	5346	-0.95	1440	4368	/	128	-1.11	/	0.09	/	634	977	/	/	0.2	0.20	458
1982	49	763	-2.75	42	661	/	6	-2.76	/	0.15	/	7	102	/	/	0.2	0.20	96
1983	4	1384	-5.85	/	720	/	14	/	/	/	/	4	662	/	/	0.2	0.20	659
1984	222	34431	-5.04	/	23207	/	165	/	/	/	/	/	11226	/	/	/	/	11226
1985	/	956	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/	/
Sum	16106	52462		12929	37751	7377	1873					2951	13754	650				12500

For the elaboration of the table see page 7-12 !
Note: Differences in sums are due to rounding errors and the occurrence of the 0-group !

Legend :
- t1 -November 1984
- t2 -November 1985
- N_{t1} -number of cod grown up within the exploited stock at the time t1
- N_{t2} -number of cod grown up within the exploited stock at the time t2
- I_{t1} -number of cod immigrated at the time t1
- I_{t2} -number of cod immigrated at the time t2
- Z_{N+I} -total mortality of the cod grown up within the exploited stock and the immigrants
- Z_N -total mortality of the cod grown up within the exploited stock
- Z_I -total mortality of the immigrants
- F'_N -number of cod grown up within the exploited stock and died by fishery
- F_N -fishing mortality of the cod grown up within the exploited stock
- F'_I -number of cod immigrated and died by fishery
- F_I -fishing mortality of the cod immigrated
- E'_N -number of cod grown up within the exploited stock and emigrated
- E_N -instantaneous emigration of the cod grown up within the exploited stock
- M_N -natural mortality of the cod grown up within the exploited stock
- M_I -natural mortality of the cod immigrated
- I' -number of cod immigrated during time t1 and t2 (instantaneous immigration)

Tab. 10 Cod stock off West Greenland. Assessment table from November 1985 till November 1986 (n x 1000).

YEAR	TOTAL $N_{t1}+I_{t1}$	$N_{t2}+I_{t2}$	Z_{N+I}	COD GROWN UP WITHIN THE EXPLOITED STOCK N_{t1}	N_{t2}	F'_N	E'_N	Z_N	F_N	E_N	M_N	IMMIGRATED COD I_{t1}	I_{t2}	F'_I	F_I	M_I	Z_I	I'
CLASS																		
1973	0	21	/	0	21	0	31	/	/	/	/	0	0	0	/	/	/	0
1974	0	0	/	0	0	0	(-16)	/	/	/	/	0	0	0	/	/	/	0
1975	20	21	-0.05	20	21	0	2	-0.05	0	0.11	-1.16	0	0	0	/	/	/	0
1976	22	22	0	12	14	1	(-89)	-0.15	0.09	0	-0.24	10	8	0	0	0.2	0.20	(-2)
1977	599	403	0.40	540	378	14	(-126)	0.36	0.03	0	0.33	60	24	1	0.02	0.2	0.22	(-24)
1978	345	94	1.30	265	74	11	32	1.28	0.04	0.13	1.11	79	20	3	0.04	0.2	0.24	(-42)
1979	6342	3441	0.61	5933	3225	916	505	0.61	0.17	0.09	0.35	410	215	61	0.16	0.2	0.36	(-71)
1980	2254	1776	0.24	2025	1717	261	2	0.16	0.14	0	0.02	228	58	9	0.04	0.2	0.24	(-121)
1981	5346	6222	-0.15	4368	5736	418	88	-0.27	0.10	0.02	-0.39	977	486	35	0.04	0.2	0.24	(-283)
1982	763	864	-0.12	661	586	45	(-5)	0.12	0.07	0	0.05	102	279	21	0.23	0.2	0.43	213
1983	1384	3892	-1.03	720	2058	4	4	-1.05	0.01	0.01	-1.07	662	1835	4	0.01	0.2	0.21	1298
1984	34431	107679	-1.14	23207	67130	/	(-104)	-1.06	/	0	/	11226	40550	/	/	0.2	0.20	31359
1985	956	10282	-2.38	/	8769	/	35	/	/	/	/	/	1513	/	/	/	/	1513
Sum	52462	134717		37751	89729	1670	699					13754	44988	134				34383

For the elaboration of the table see page 7-12 !

Note: Differences in sums are due to rounding errors and the occurrence of the 0-group !

Legend :
- t1 -November 1985
- t2 -November 1986
- N_{t1} -number of cod grown up within the exploited stock at the time t1
- N_{t2} -number of cod grown up within the exploited stock at the time t2
- I_{t1} -number of cod immigrated at the time t1
- I_{t2} -number of cod immigrated at the time t2
- Z_{N+I} -total mortality of the cod grown up within the exploited stock and the immigrants
- Z_N -total mortality of the cod grown up within the exploited stock
- Z_I -total mortality of the immigrants
- F'_N -number of cod grown up within the exploited stock and died by fishery
- F_N -fishing mortality of the cod grown up within the exploited stock
- F'_I -number of cod immigrated and died by fishery
- F_I -fishing mortality of the cod immigrated
- E'_N -number of cod grown up within the exploited stock and emigrated
- E_N -instantaneous emigration of the cod grown up within the exploited stock
- M_N -natural mortality of the cod grown up within the exploited stock
- M_I -natural mortality of the cod immigrated
- I' -number of cod immigrated during time t1 and t2 (instantaneous immigration)

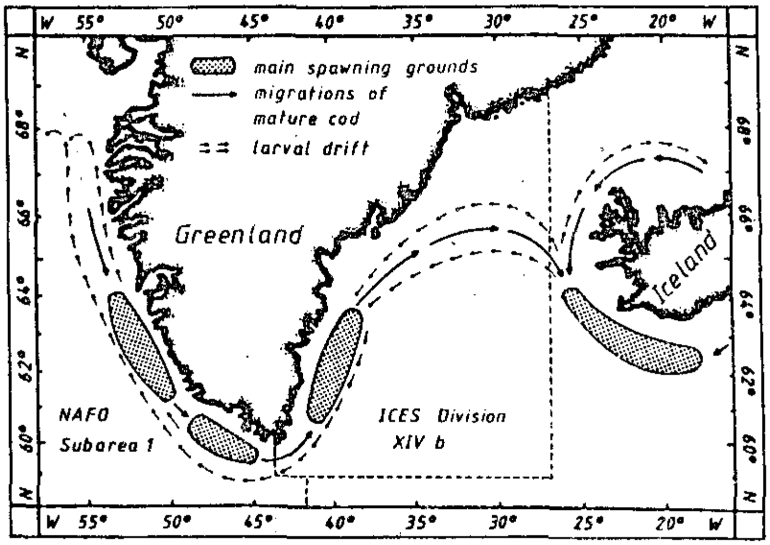


Fig. 1 Cod stock complex West Greenland, East Greenland and Iceland (Anon., 1987). The cod stocks off West and East Greenland are related to the convention areas of the NAFO (Subarea 1) and the ICES (Division XIVb).
------ Boundaries of the convention areas.

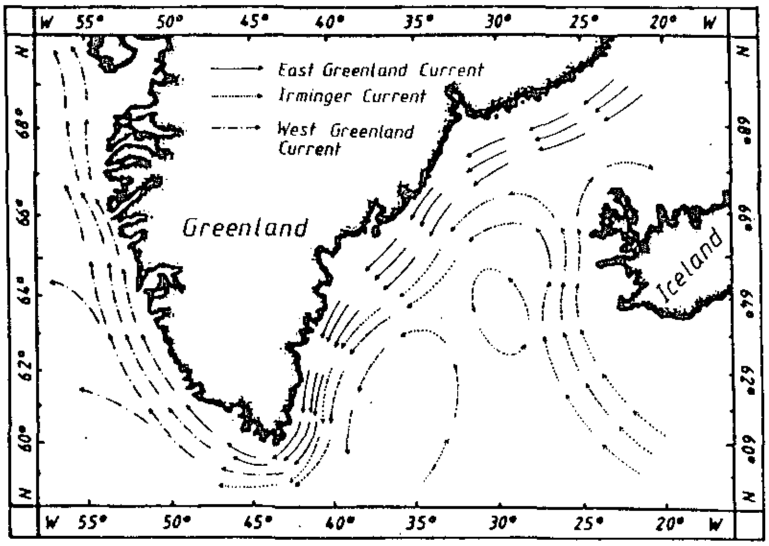


Fig. 2 The sea current round Greenland (Kiilerich, 1943; Hackey et al., 1954; Dietrich, 1957).

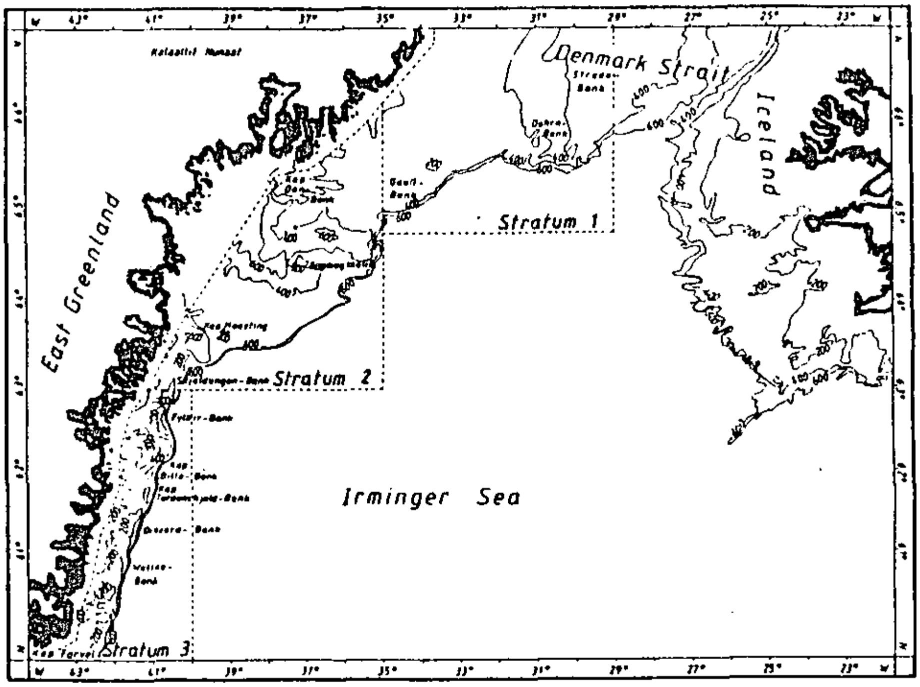


Fig. 3 Topography of the Irminger Sea. Areas of investigation (strata 1-3).

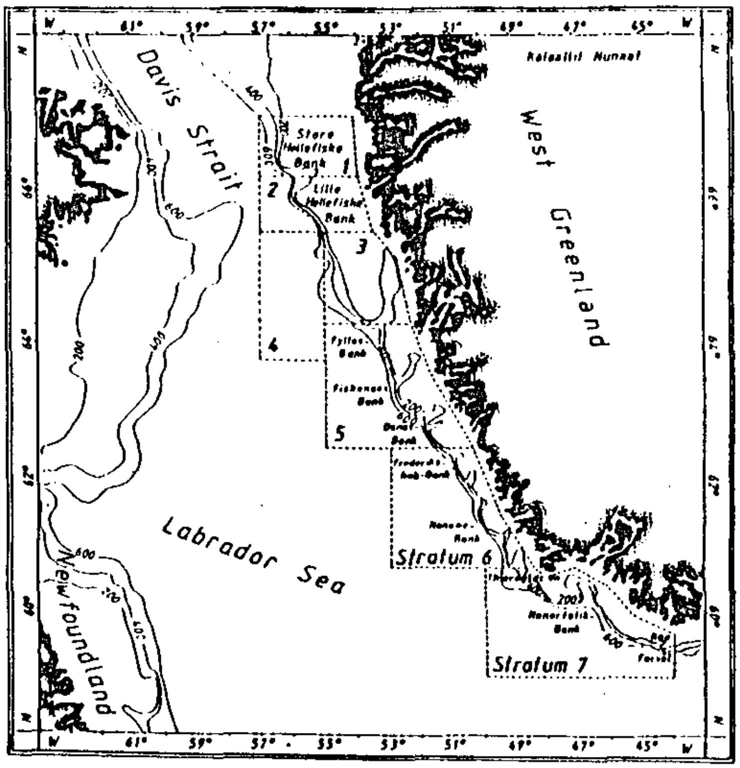


Fig. 4 Topography of the Labrador Sea. Areas of investigation (strata 1-7).

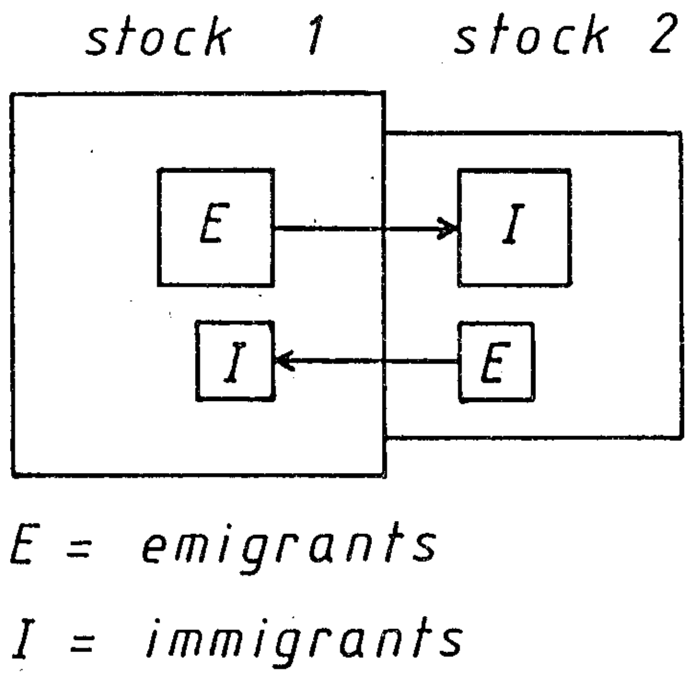


Fig. 5 Schematic illustration of the migration between two stocks considered in the calculation model.

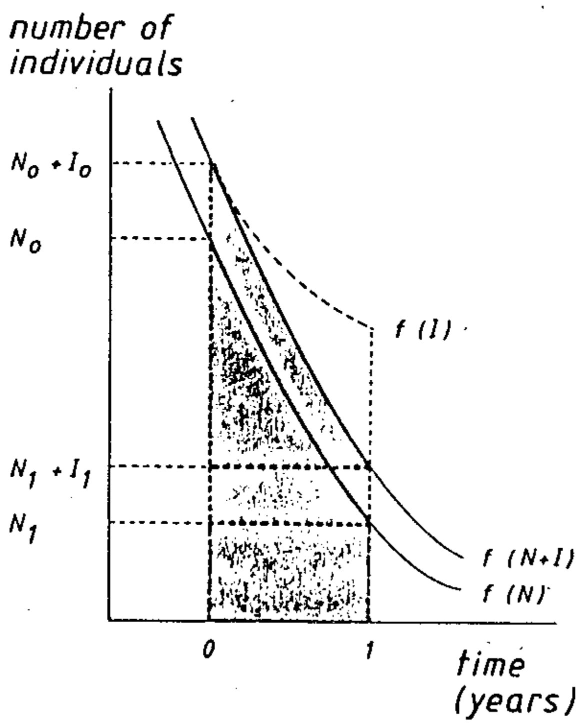


Fig. 6 Functions of the decrease of individuals within a single year class.
N=number of individuals grown up in the stock unit
I=number of immigrants

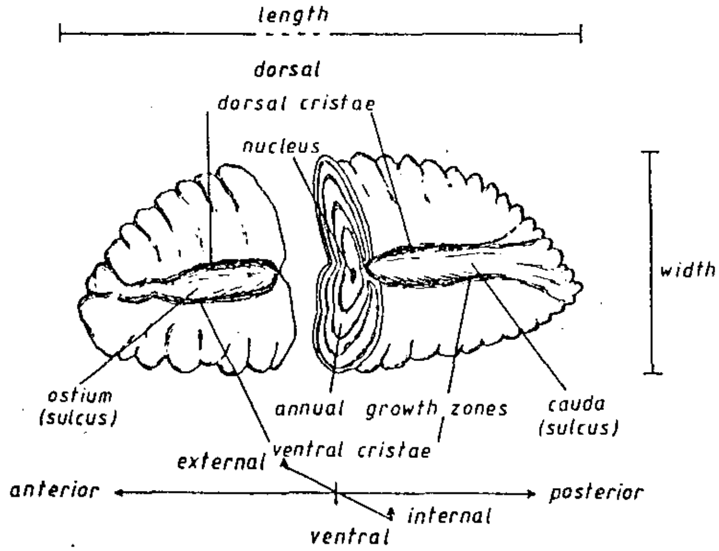


Fig. 7 The inner face of the right sagitta (homosulcoid, pseudobiostial; Schwarzhans, 1978).

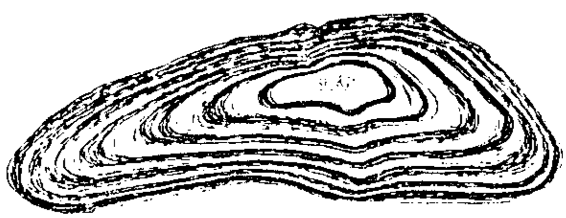


Fig. 8 Annual growth zones type A. Top view on the surface of cut of a cod otolith showing 7 annual growth zones type A. On graphic-technical grounds the opaque zones are white and the hyaline zones are black.

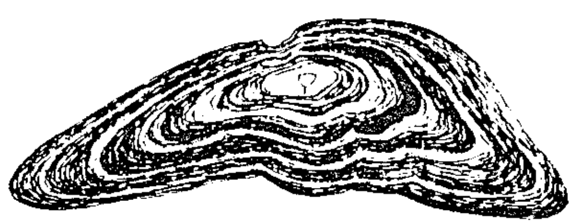
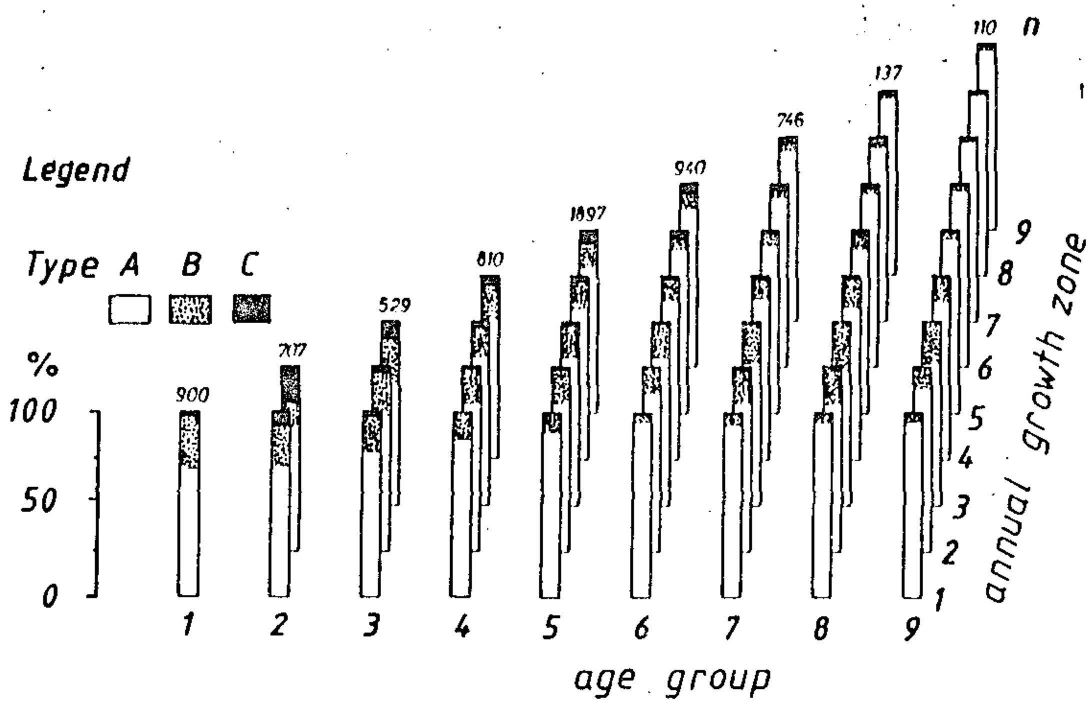


Fig. 9 Annual growth zones type B. Top view on the surface of cut of a cod otolith showing 5 annual growth zones type B. On graphic-technical grounds the opaque zones are white and the hyaline zones are black.

West Greenland



East Greenland

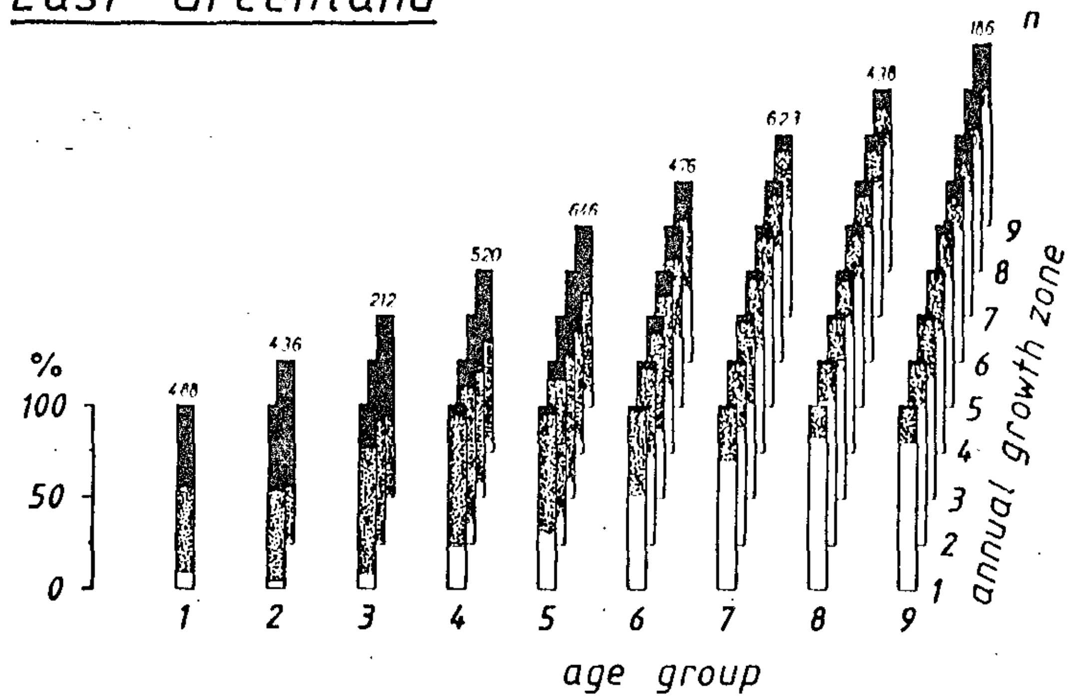


Fig. 10 Percentage occurrence of the types of annual growth zones.

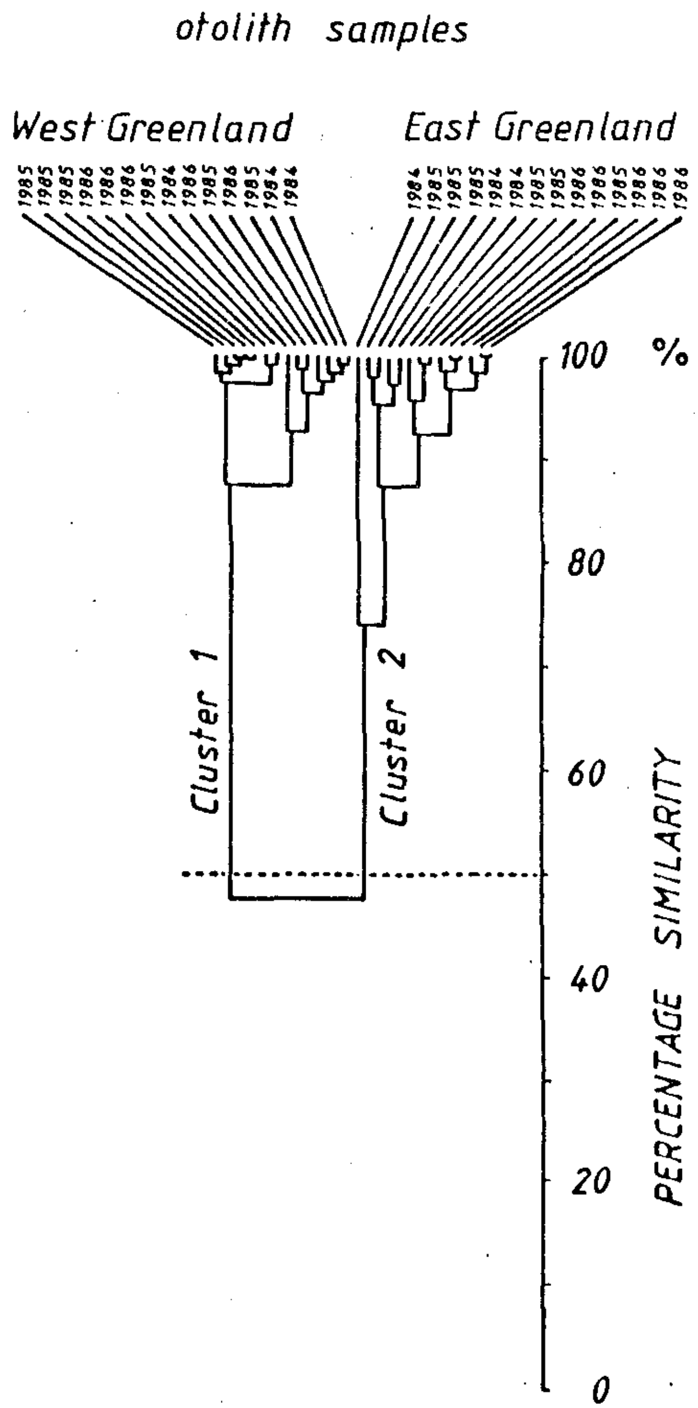


Fig. 11 Cluster analysis of otolith samples from 1984-86 (dendrogram). The similarities between the samples are illustrated (coefficient of percentage similarity, average linkage method).

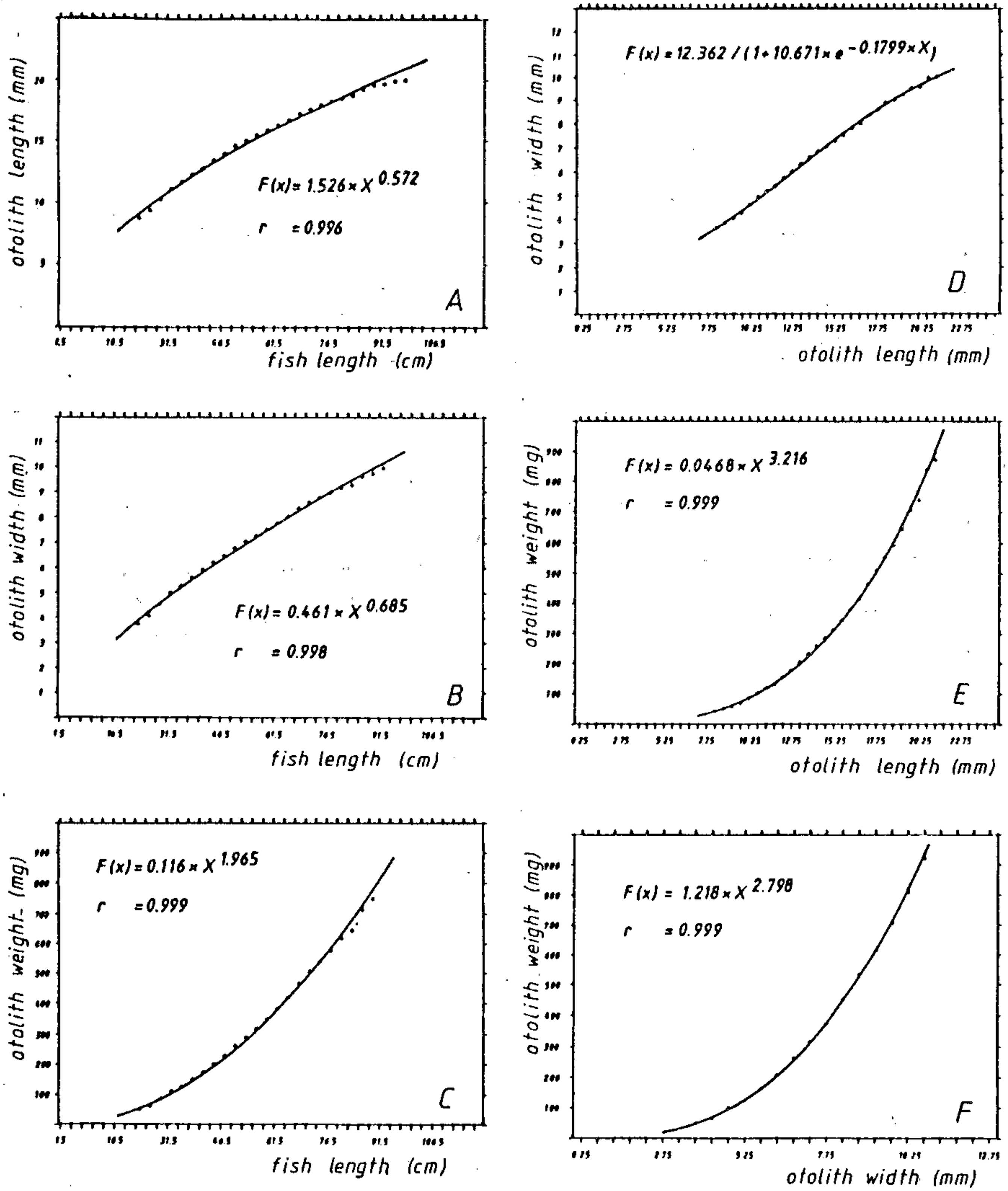


Fig. 12 Cod off Greenland. Relative Growth.
A otolith length / fish length
B otolith width / fish length
C otolith weight / fish length
D otolith width / otolith length
E otolith weight / otolith length
F otolith weight / otolith width

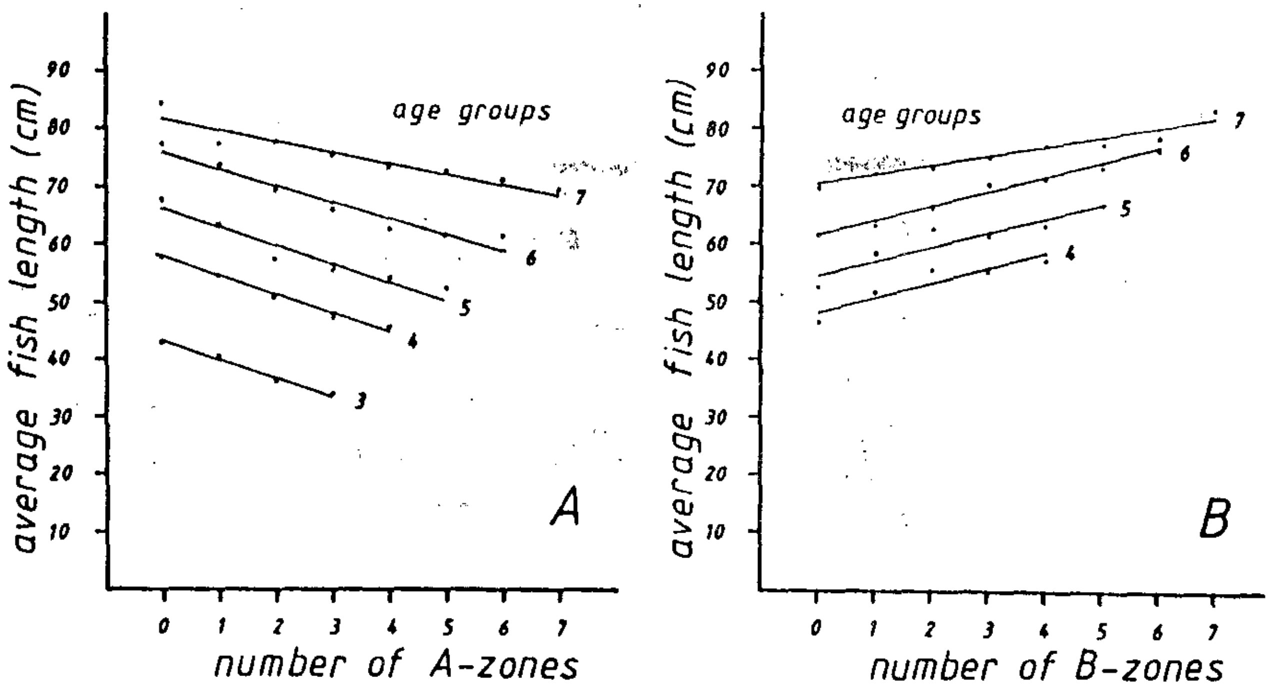


Fig. 13 Cod off Greenland. Average fish length per age group in relation to the number of A-zones (A) and the number of B-zones (B) in the otoliths.

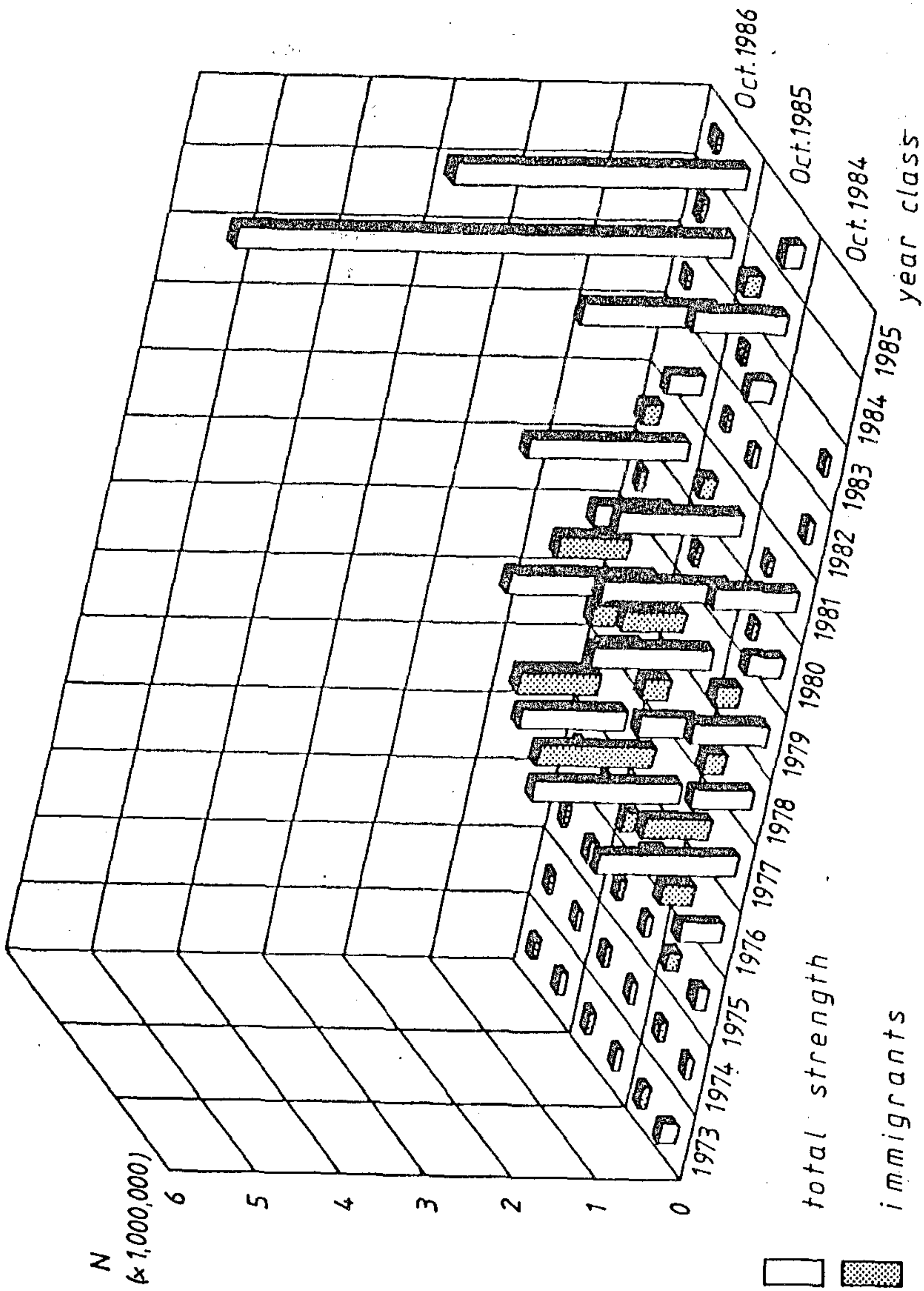


Fig. 14 Cod stock off East Greenland. Strength of year classes and numbers of immigrants.

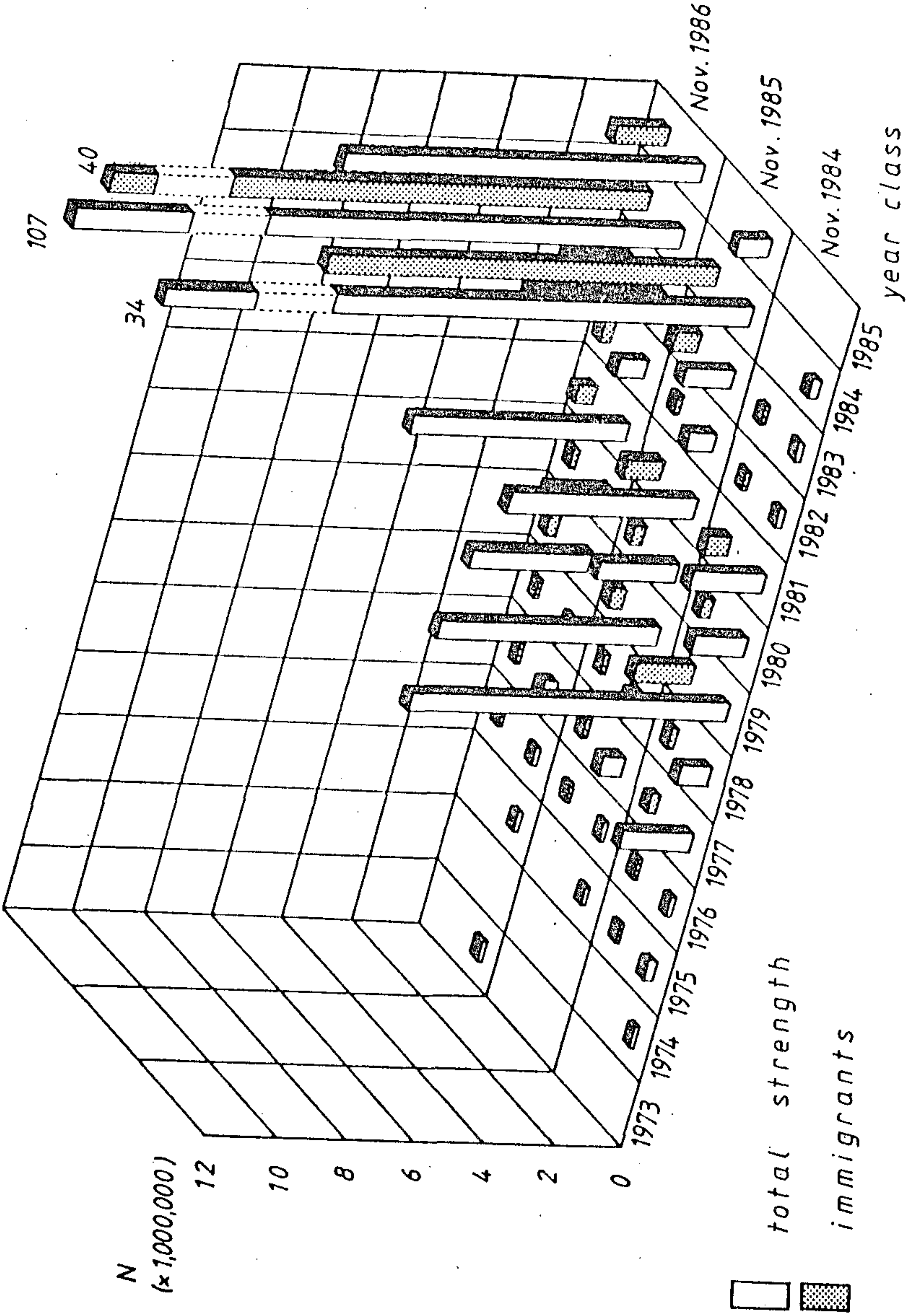


Fig. 15 Cod stock off West Greenland. Strength of year classes and numbers of immigrants.