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Variation in Growth and Recruitment of Atlantic Cod (*Gadus morhua*) off Greenland During the Second Half of the Twentieth Century

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Abstract

The variation in length-at-ages 4 to 5 years for Atlantic cod off Greenland was analysed based on a time series of samples taken from commercial catches comprising 190 000 individual age determinations. Multiple linear regressions revealed significant declines in size for these age groups since mid 1950s by 10 and 5 cm, respectively. The growth models considered temperature, fishing mortality and stock abundance effects, all of them expressed as means over the life span of individual year classes. The positive temperature and negative fishing mortality effects were found to dominate the variation in length-at-age. However, the analyses did not indicate a negative effect of stock density on cod growth.

During the period 1956-89, the number of recruits at age 3 years were identified to be significantly correlated with the spawning stock biomass and June water temperature on top of Fyllas Bank (West Greenland). Both factors positively affected the number of offsprings and explained 51 % of the observed variation in recruitment.

Introduction

Since the early 1920s, the marine life on the shelves and continental slopes off Greenland has been significantly affected by fishing activities. Until 1990, multi-national fleets directed their effort mainly to Atlantic cod (*Gadus morhua*), golden and deep sea redfish (*Sebastes marinus* and *S. mentella*). After the collapse of these offshore stocks, the shrimp (*Pandalus borealis*) and Greenland halibut *(Reinhardtius hippoglossoides)* fisheries remained as the only ones of commercial importance.

The cod stock off Greenland, for a long time being considered the main commercial and biological species of the area, collapsed at the end of the 1960s decade and remained at a very low level since then (Anon., MS 1996). Cod abundance and spawning stock biomass have declined by almost 100 % from the initial levels observed during the mid 1950s when annual exploitation rates exceeded 300 000 tons for the first time. In addition to this major anthropogenic effect, studies on climatic and oceanographic conditions around Greenland (Buch and Stein, 1989) revealed concomitant interannual changes in the ocean and atmosphere which might have influenced fish biomass production in this area (Buch et al., 1994).

The main goal of the present investigation is to identify factors associated with the progressive commercial extinction of cod off Greenland. Constrained by the data available we focussed our analyses on variation in length-at-age related to temperature, exploitation rates and fish density, and on recruitment variation related to temporal changes in spawning stock biomass and water temperature. Year to year variations of mean length-at-age and recruitment are affected by a combination of fishery, physical and biotic effects and have direct consequences for fish biomass production and management. However, the variation of these vital stock parameters seems to be inadequately incorporated in long-term harvest strategies.

Materials and Methods

Interannual Variation in Length-at-Age

Since 1955, length data and age determinations were sampled from German commercial cod catches off East Greenland (ICES Div. XIVb) and West Greenland (NAFO Div. 1B-1F). Measurements and otolith collections were conducted directly on board the fishing vessels or derived from fresh fish landings at fish markets. The sampling strategy on fish markets was stratified by fish size categories of landings, raised by the weight of the various categories, and added to represent the length composition of the landed catch by vessel. Length data measured on board the fishing vessels represented the sum of analysed catches according to the catch weight. The sampling program comprised a total of 746 samples of length measurements and 190 505 individual age determinations. Length measurements were performed with a precision of one centimetre (cm below). One of both sagitta otoliths was removed from the fish and stored in paper bags for age determination purposes. The individual otoliths were cutted through the central region and aged under a binocular microscope applying the method of transmitted light (Meyer, 1965).

Length-at-age data do not only vary interannually but are also subject to quarterly and areal effects. Therefore, length and otolith samples were aggregated by quarter (1955-91) for East and West Greenland separately. Mean length-at-age was calculated by applying the length-age-keys to the length composition of the catches for each quarter and both areas. Only mean length-at-age values based on 10 and more age determinations were considered sufficiently precise and used in the present investigations. In order to eliminate the quarterly effect, mean length-at-ages 4 to 11 years observed in the first, third, and fourth quarter were converted to expected values in the second quarter by means of adding or substracting quarterly growth increments as calculated from significant linear regressions. For each year, the converted and the observed mean length-at-ages 4 to 11 in the second quarter were averaged to represent single annual values during the period of investigation. Both data sets for East and West Greenland were combined to one matrix by the calculation of weighted means according to the proportion caught in numbers off East and West Greenland (Horsted, MS 1994).

In order to reduce the effect of errors in age determination, length-at-age data were smoothed by fitting v. Bertalanffy (1938) growth functions for the year classes 1955 to 1981. The parameters of the functions are listed in Table 1. The good fit between observed and calculated length-at-age data is confirmed by the resulting high r-squared values. Missing data in Table 1 indicate a poor fit of the v. Bertalanffy growth function to the length-at-age measurements for few year classes which were disregarded in the analyses. The length-at-ages 4 and 5 as derived from the v. Bertalanffy growth funcions are also listed in Table 1.

The interannual variation of the length-at-ages 4 and 5 years of the year classes 1955 to 1981 was finally analysed by fitting univariate and multiple linear regression models based on temperature, stock size, and fishing mortality effects, all of them expressed as mean values over the life span of individual year classes, respectively. Stock size estimates for ages 3 years and older and coefficients of fishing mortality rates were adopted from the most recent analytical assessment (Anon., MS 1996; Rätz, 1997).

Interannual Variation in Recruitment

Estimates of spawning stock biomass (SSB) and recruits at age 3 years were also adopted from the virtual population analysis (VPA) conducted by the ICES North-Western Working Group in 1996 (Anon., MS 1996; Rätz, 1997). The VPA was based on international offshore catches only and calibrated by the German age disaggregated survey data (Rätz, MS 1996). Historic data revealed that cod off Greenland mature at ages 5 to 7. Numbers of recruits at age 3 years were taken as an estimate of year class strength at age 0 in order to meet the conditions in the particular years of birth. We used the method of multiple linear regression in order to formulate a recruitment model based on SSB and temperature effects. Respective values are listed in Table 2.

Water Temperature

Water temperatures on the top of Fyllas Bank off West Greenland (Stein, MS 1988) were sampled by the Greenland Fisheries Research Institute, Copenhagen during mid-June of each year since 1950. The mean temperature of the surface layer was derived by averaging the observations at the standard levels, 0, 10, 20, 30 and 40 m. Buch (1984) showed that the temperature trends in neighbouring areas and periods were similar to those on Fylla Bank due to the process of advection and solar heating. Therefore, the mid-June temperature regime on Fylla Bank is considered to be representative index of the thermal conditions in the shelf region off West Greenland (Hansen and Buch, 1986).

Results

Interannual Variation in Length-at-Age

The various year classes displayed a high variation in growth. The estimates of $L_{infinity}$ ranged from 87 to 226 cm (Tab. 1). The coefficients k representing the growth rates of the individual year classes were rather small and varied between 0.06 and 0.34. The time series of mean length-at-ages 4 and 5 showed an overall decreasing trend with high variations since the stock collapsed at the end of the 1960s. Mean length-at-ages 4 and 5 declined from 61 and 67 cm in 1959 and 1960 to 43 and 53 cm in 1985 and 1986, respectively.

Mean length-at-ages 4 and 5 were found to be correlated with the temperature. Fish sizes increased significantly with increasing water temperature on top of Fyllas Bank (Fig. 1). The temperature explained 33 and 15 % of the observed variation in mean length-at-ages 4 and 5, respectively. Stronger and negative correlations between observed fish sizes were found using mean fishing mortality. The fish were found to be significantly smaller in years with high exploitation rates which explained 42 and 32 % of the observed variation for both age groups analysed (Fig. 2). The strongest effects were indicated from linear correlations for fish size at age versus stock abundance including age groups 3 and older. 4 and 5 year old cod were big when the stock abundance was high (Fig. 3). The positive density effect accounted for 46 and 33 % of the observed variation in length.

The individual relations between variations in mean lenght at ages 4 and 5 (dependent) and mean temperature over life span (independent), mean fishing mortality (independent) and mean stock size in number (independent) were combined to multiple linear regression models. The models explained 54 and 36 % of the observed variation in mean fish size, respectively. Both models were specified in Table 3 and illustrated in Figures 4 and 5.

Interannual Variation in Recruitment

From 1955 to 1989, the cod stock off Greenland has undergone important demographic changes. Both spawner biomass and recruitment declined by nearly 100 % when comparing initial and final estimates (Tab. 2). The spawning stock biomass and number of recruits at age 3 collapsed from 1.8 million tons and 134 million to 250 000 tons and 25 million in 1972, respectively. Since then, the estimates varied at this low level and continued to decline with the exception of the two strong year classes 1973 and 1984 which did not contribute to an increase in the spawning stock biomass.

Figure 6 shows the scatter plot of estimates of recruits at age 3 versus the water temperature observed on top of Fyllas Bank. The resulting r^2 betweeen both variables amounted to 0.20 indicating a significant positive effect of temperature on the number of stock offsprings. Also the spawning stock biomass was found to be significantly correlated with the recruitment (r^2=0.41). The scatter plot in Figure 7 illustrates that the estimated variation in spawning stock biomass has a higher explanatory weight for recruitment strength than the temperature variation.

We formulated a multiple linear regression model for the numbers of recruits at age 3 (dependent) based on the positive temperature (independent) and spawning stock biomass (independent) effects. This model is specified in Table 4 and explained 51 % of the variation in year class strength at age 3. For the period of investigation, the fit between observed and model predicted values is illustrated in Figure 8.

Discussion

Interannual Variation in Length-at-Age

Our analyses revealed significant reductions in mean length of Atlantic cod off Greenland at ages 4 and 5 since mid 1950s by 10 and 5 cm, respectively. Similar declines in size-at-age have been documented for the cod stocks around the Faroe Islands (í Jákupsstovu and Reinert, 1994) and off Labrador (Shelton and Morgan, 1994). We investigated the age groups 4 and 5 due to their major shares in catch in number throughout the period of investigation. Since the late 1960s when the stock collapsed, size estimations of older fish were probably less representative due to their rarity in the catches. It should be outlined that the raw data were derived from commercial catches and could not be corrected for small scale areal and depth effects which are considered to contribute significantly to the observed variation (Jørgensen, 1992). However, multiple linear regressions suggest that size at ages 4 and 5 years are positively affected by temperature and stock abundance while the fishing mortality was identified to have a negative effect (Tab. 3, Fig. 4 and 5). Our analyses are based on arithmetic means of the temperature, stock abundance and fishing mortality over the life span of the cohorts in oder to reflect their long-term effects on growth rates. These models (multiple linear regression) are highly significant and explained 54 and 36 % of the observed variation in length-at-ages 4 and 5. However, the explanatory power of the model is weakened by low statistical co-linearity of the independent variables.

Since decades, the influence of environmental conditions on growth of cod has been a central question in fisheries biology and has attracted scientific interest (Taylor, 1958). Most authors (e.g Hansen, 1949; Dementyeva and Mankevich, 1965; Jónsson, 1965; Jørgensen, 1992; Nakken, 1994; Brander, 1995) have found positive regressions between temperature and fish size at age which were also apparent from the analyses presented here. Brander (1995) concluded that year-to-year variation in weight-at-age of cod within and between stocks might be largely controlled by water temperature and highlighted the importance in respect of stock and catch assessments and resulting predictions used for management purposes. In addition to the direct effect of temperature on the growth physiology of poikilothermic animals (assimilation, metabolism, transformation, and excretion; Brett, 1979) there should be indirect effects considered such as changes in food quality or availability. Jørgensen (1992), Nilssen et al. (1994), and Steinarsson and Stefanson (MS 1991) demonstrated positive effects of the capelin (*Mallotus villosus*) abundance on the growth rates of Arcto-Norwegian and Icelandic cod, the main food item of these stocks.

Supposing the existence of intra-specific competition, fish density was always considered to be an important factor determing growth rates. Theoretically, the growth rates should decrease with increasing abundance (Hempel, 1957). The results of the present study do not support this idea. In the case of the North Sea cod there were also no clues for environmental or density effects providing a likely explanation (Daan et al., 1994). In our case the lack of a density-dependent growth remains difficult to explain since pronounced inverse abundance effects were reported from the Northeast Arctic (Nilssen et al., 1994) and Icelandic stocks (Schopka, 1994).

During periods of intensive exploitation as indicated by high fishing mortalities, the Atlantic cod off Greenland at age 4 and 5 were found to be very small. These results do not reflect necessarily changes in growth rates but point at a higher selection of the fast growing individuals by the fishery. Exploitation rates which frequently exceeded 70 % of the fishable stock (Anon., MS 1996) over the past 40 years support the idea of higher survival rates of slow growing individuals.

Interannual Variation in Recruitment

Since more than 50 years, fisheries biologists focussed their interest in the role of the spawning stock biomass (SSB) and the temperature as determinant factors of the fish recruitment (Berverton and Holt, 1957; Cushing, 1972; Ricker, 1975). Nowadays, the size of the SSB is generally accepted as a very important indication for the exploitation status of the majority of marine fish stocks (Anon., MS 1997; Serchuk et al., MS 1997). Our analyses identified both water temperature and SSB as important factors for the reproductive success of the cod stock off Greenland. The developed model (multiple linear regression) based on these two independent variables explains 51 % of the observed variation in 3 years old offsprings during 1955-89 and quantifies the explanatory weight of the SSB effect as dominant (Tab. 4, Fig. 8). Thus, our results provide strong evidence that the collapse of the cod stock off

Greenland in the late 1960s was mainly due to the progressive extinction of the spawners by fishing activities (Rätz, 1997). In particular, the model indicates the importance of a high SSB at the northern limit of cod distribuiton in order to compensate for adverse environmental effects on recruitment success. Before the stock collapsed in the late 1960s, recruitment was highly variable and failed in some years even with high SSB but there were only two strong year classes produced during the past 30 years, namely the 1973 and 1984 year classes. The model fit increases significantly to 59 % by omission of these strong year classes. The year classes 1973 and 1984 are supposed to be of Icelandic origin and have drifted in the Irminger current to Greenland nursery grounds (Vilhjálmsson and Friðgeirsson, 1976; Vilhjálmsson and Magnússon, MS 1984).

The sudden decline of SSB was an important factor during the collapse of northern cod of Newfoundland and Labrador in the early 1990s (Hutchings and Myers, 1994). In addition, the environmental parameters are considered to contribute significantly to cod recruitment success (Lear and Parsons, 1993; de Young and Rose, 1993). Evidence of biotic and physical influences on Northeast Arctic cod recruitment has been documented by Ottersen and Sundby (1995) and Nilssen et al. (1994). They identified positive effects of SSB and temperature on year class strength in a similar magnitude as determined in the present analysis.

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Table 1. Parameters of the v. Bertalanffy growth functions (t_o, L_{inf}, k) for year classes 1955-81, r^2 between observed and calculated mean length-at-ages 4-11, water temperature, stock abundance ages 3+ and mean fishing mortality F at ages 5-8 (Anon., MS 1996).

Year class/ Year	t_o	L_{inf} (cm)	k	r^2 Lobs-Lcalc	Length (cm) at age 4 calculated	Length (cm) at Age 5 calculated	Temp. (°C)	Stock 3+ (millions)	Fmean 5-8
1955	-3.101	162.9	0.062	0.913	60.8	67.0	1.2	1341.1	0.109
1956							0.9	1427.3	0.149
1957	0.060	100.9	0.176	0.993	53.9	61.5	2.3	1115.6	0.210
1958	-1.143	115.2	0.115	0.991	54.3	60.9	2.2	994.1	0.202
1959	-2.877	154.3	0.060	0.994	54.5	60.3	1.6	1087.2	0.189
1960	-0.105	104.3	0.151	0.996	51.5	58.9	2.7	1332.2	0.194
1961	-0.460	104.5	0.142	0.999	52.1	59.0	3.2	1224.7	0.257
1962	-0.864	111.0	0.115	0.989	50.5	57.1	2.2	956.2	0.404
1963							1.6	1016.6	0.369
1964	-0.050	115.1	0.117	0.879	46.8	54.4	2.3	1385.6	0.387
1965							2.1	1301.3	0.411
1966	2.357	106.7	0.216	0.913	38.1	51.4	1.6	1240.3	0.402
1967	-0.639	225.5	0.048	0.980	48.2	56.4	1.5	954.2	0.414
1968	0.657	151.2	0.101	0.995	47.6	57.6	2.1	643.7	0.440
1969	2.603	99.0	0.313	0.981	42.6	57.8	0.3	406.0	0.379
1970							0.3	264.1	0.219
1971	2.086	110.1	0.249	0.950	48.3	61.9	0.8	251.2	0.398
1972	1.152	126.8	0.144	0.981	47.4	58.1	0.6	160.6	0.473
1973	1.055	99.4	0.202	0.992	48.8	58.0	1.7	101.9	0.431
1974	1.043	102.2	0.161	0.961	42.7	51.6	1.4	53.3	0.670
1975	0.655	100.7	0.153	0.934	43.9	52.0	1.9	50.7	0.906
1976	2.591	87.3	0.340	0.993	40.1	53.7	1.4	181.7	0.821
1977	-0.069	136.3	0.094	0.989	46.9	55.0	2.2	140.1	0.764
1978							0.9	112.9	0.267
1979	1.040	139.3	0.112	0.928	43.6	53.7	2.3	100.5	0.294
1980	2.894	97.5	0.268	0.851	32.3	47.6	1.9	143.4	0.502
1981	1.159	122.7	0.134	0.887	43.3	53.3	1.6	107.8	0.414
1982							0.8	127.2	0.751
1983							0.4	82.3	0.913
1984							1.0	54.9	0.686
1985							2.1	32.4	0.241
1986							2.2	33.0	0.159

Table 2. Estimates of spawning stock biomass, water temperature, and recruits at age 3 years (Anon., MS 1996), 1955-89.

Year class/ Year	SSB (1 000 t)	Temp. (°C)	Recruits at Age 3 (millions)
1955	1817.5	1.2	134.5
1956	1519.5	0.9	463.7
1957	1331.3	2.3	531.7
1958	1469.3	2.2	226.9
1959	1042.4	1.6	93.6
1960	1228.8	2.7	409.6
1961	1083.5	3.2	703.4
1962	1035.9	2.2	286.7
1963	1020.4	1.6	330.0
1964	887.2	2.3	105.6
1965	716.2	2.1	37.5
1966	715.5	1.6	39.1
1967	828.7	1.5	22.8
1968	775.9	2.1	88.0
1969	572.0	0.3	4.2
1970	467.0	0.3	9.2
1971	378.3	0.8	6.2
1972	248.1	0.6	24.6
1973	109.5	1.7	154.6
1974	88.9	1.4	16.6
1975	54.8	1.9	20.1
1976	30.1	1.4	26.8
1977	20.6	2.2	71.1
1978	37.8	0.9	14.3
1979	78.8	2.3	56.5
1980	94.1	1.9	7.7
1981	71.1	1.6	13.8
1982	57.2	0.8	2.0
1983	46.6	0.4	10.9
1984	35.6	1.0	265.7
1985	29.9	2.1	85.1
1986	32.9	2.2	1.4
1987	36.2	2.1	1.6
1988	56.4	2.0	0.6
1989	83.6	0.9	0.3

Table 3. Results of multiple linear regression analyses between length-at-ages 4 and 5 years (cm. dependent) and mean water temperature (°C. independent). mean F ages 5-8 (independent) and mean stock abundance (ages 3+ in millions. independent) over life span. All parameters are significant at $p<0.01$.

Length-at-age (cm)	n	a	Temperature (°C)	Fmean (5-8)	Stock 3+ (millions)	r^2
			b	b	b	
4 years	22	47.753	4.301	-17.721	0.001	0.541
5 years	22	59.205	1.183	-11.543	0.001	0.355

Table 4. Results of multiple regression between recruitment at age 3 (million, dependent) and water temperature (°C, independent) and SSB (1 000 tons, independent). All parameters are significant at $p<0.01$.

Recruits at age (millions)	n	a	Temperature (°C)	SSB (1000 t)	r^2
			b	b	
3	35	-99.485	78.240	0.185	0.508

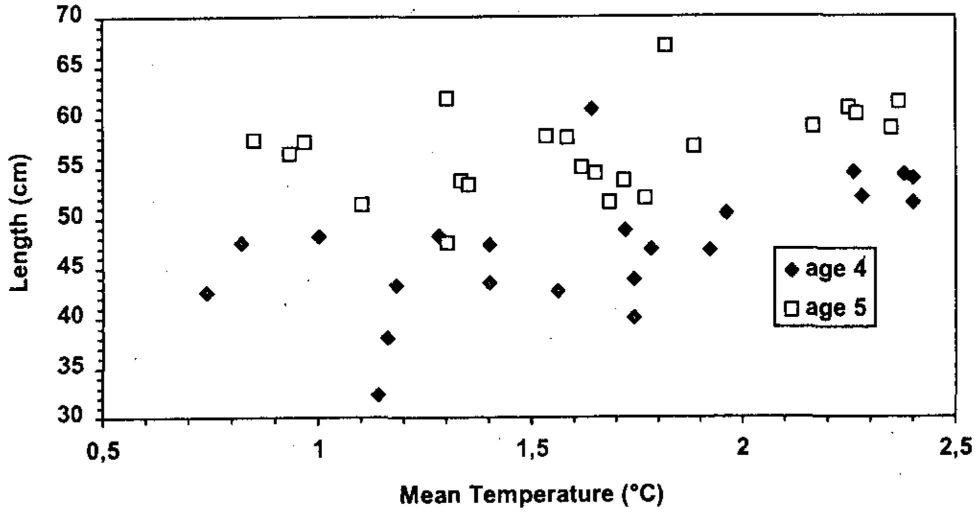

Fig. 1 Scatter plot of mean June water temperature over life span of the individual year classes versus their mean length-at-ages 4 and 5 ($r^2_{age\ 4}$=0.33; $r^2_{age\ 5}$=0.15).

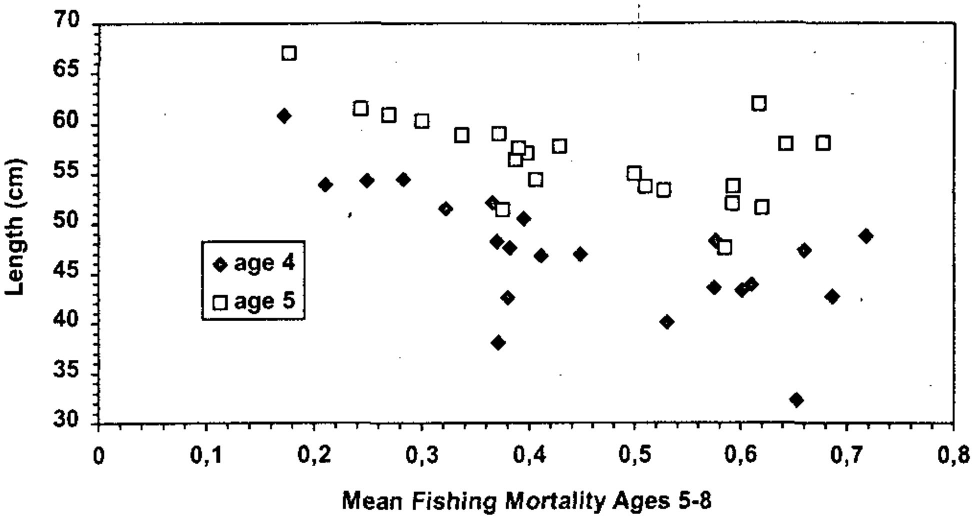

Fig. 2 Scatter plot of mean fishing mortality ages at ages 5-8 over the life span of the individual year classes versus their mean length-at-ages 4 and 5 ($r^2_{age\ 4}$=0.42; $r^2_{age\ 5}$=0.32).

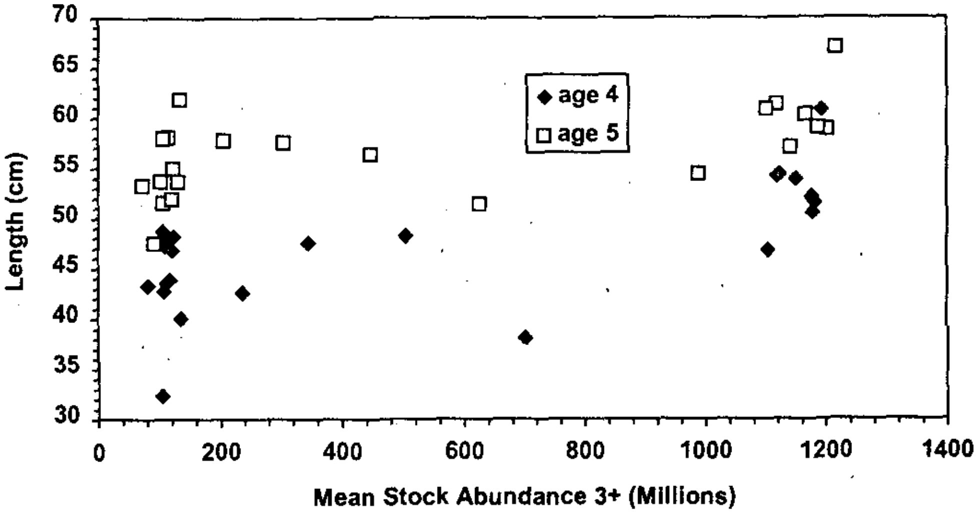

Fig. 3 Scatter plot of mean stock abundance 3+ over the life span of the individual year classes versus their mean length-at-ages 4 and 5 ($r^2_{age\ 4}$=0.46; $r^2_{age\ 5}$=0.33).

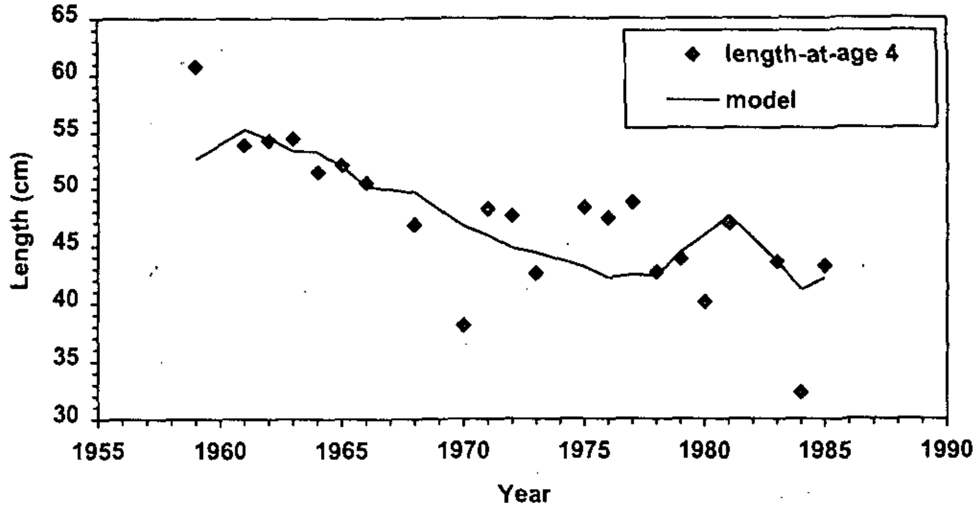

Fig. 4 Length-at-age 4 years as observed in commercial catches and derived from the multiple linear regression model (Tab. 3). 1959-85.

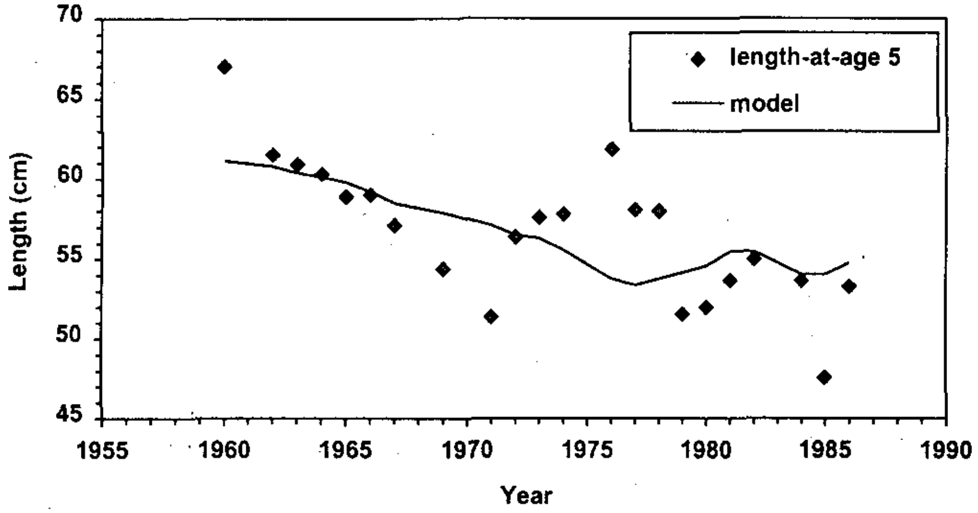

Fig. 5 Length-at-age 5 years as observed in commercial catches and derived from the multiple linear regression model (Tab. 3). 1960-86.

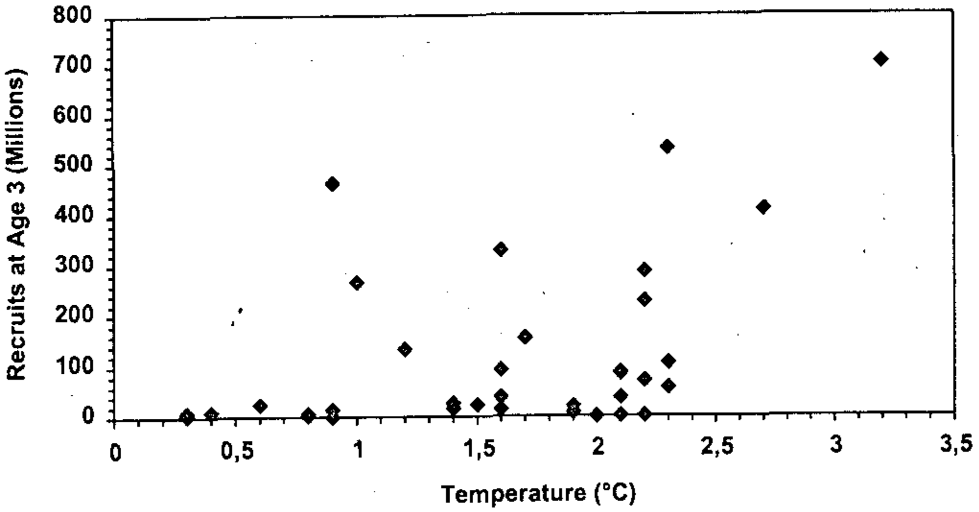

Fig. 6 Scatter plot of June water temperature versus recruits at age 3 (r^2=0.20). 1955-89.

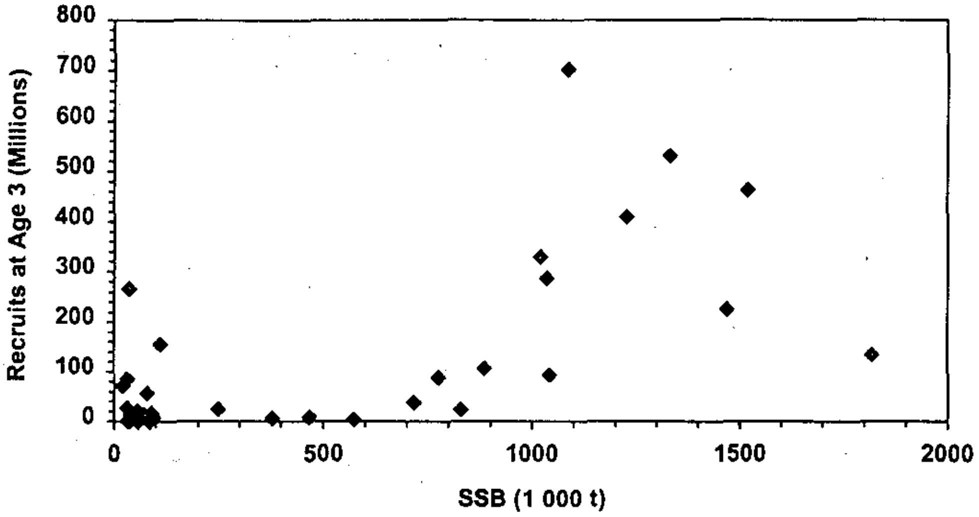

Fig. 7 Scatter plot of spawning stock biomass (SSB) versus recruits at age 3 (r^2=0.41). 1955-89.

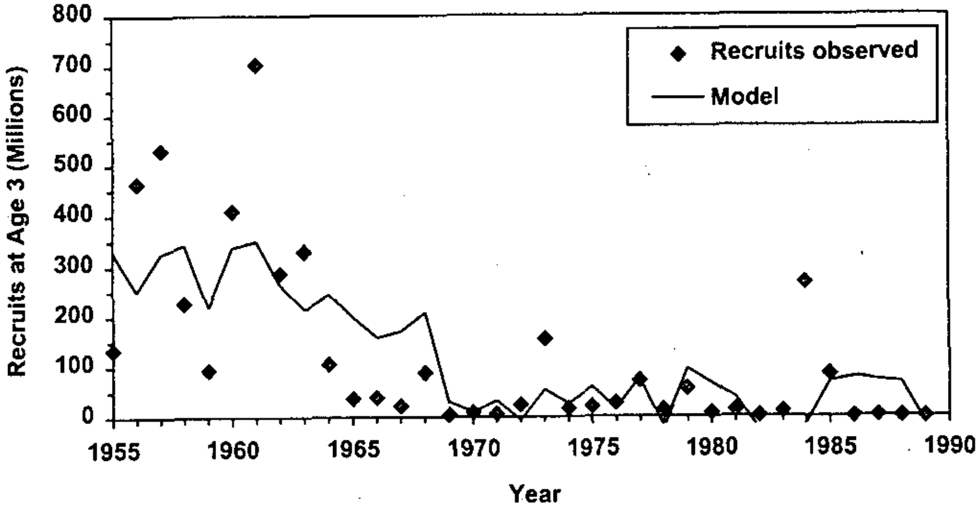

Fig. 8 Recruitment variation and fit of the multiple linear regression model (Tab. 4). 1955-89.