International Council for the Exploration of the Sea

CM 1995/P:10
Theme Session on Causes of Observed Variations in Fish Growth

GROWTH OF ARCTO-NORWEGIAN COD IN DEPENDENCE OF ENVIRONMENTAL CONDITIONS AND FEEDING

by

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ABSTRACT

Variability of length and weight of 3-9-year cod from the southern part of the Barents Sea (ICES area 1) is analysed with the use of data for 1949-1991 and statistical methods. In year-to-year variations of length and weight, quasi-cyclic fluctuations with periods of about 6-8 and 11-14 years are revealed. Asynchronous statistically significant relations between cod length and water temperature and capelin abundance are also revealed. Temperature contributes more into the length variance than capelin, whereas year-to-year changes of weight are caused by capelin abundance fluctuations more than by water temperature. Seasonal migrations of of cod and capelin are analysed. It is shown that cod consumption of capelin has two maxima a year (in February-May and August-October), caused by the largest overlapping of species habitats. Minimal capelin content in cod stomachs are observed in November-January and June-July. Capelin are the least accessible for cod in these periods. Due to data for 1953-1991 on frequency of occurrence (%) of fish consumed capelin, young cod and redfish, as well as shrimp and euphausids, year-to-year food changes of cod and their effect on weight and length growth, are analysed. Multiple linear regression models, describing satisfactorily year-to-year variations of cod length and weight, are created.

INTRODUCTION

Studying of cod growth variability is scientifically and practically important. Data on mean weight of cod are used in modelling of abundance dynamics and in calculation of total allowable catch (TAC) of cod. Besides, mean weight of cod are accounted in determination of capelin amount consumed by cod and in calculation of capelin TAC.

Main factors influencing cod growth are feeding conditions, water temperature and density of cod population (Rollefsen, 1938, 1954;

Saetersdal and Cadima, 1960; Dementyeva and Mankevich, 1965: Ponomarenko, 1968; Borisov, 1978; Nilssen et al., 1993; Cardenas, 1994). Food gives energy and nutrients to an organism. Water temperature fluctuations speed up or slow down metabolism. Under other constant conditions, populational density changes can influence the growth rate through the feeding competition. Significance of some factors and their contribution into the variance of growth indices varies by years and periods.

The aim of the paper is to analyse year-to-year variations of length and weight of Arcto-Norwegian cod, to estimate the effect of some factors on these changes and to build regression models for length and weight.

MATERIALS AND METHODS

Materials were data on length and weight of 3-9-year cod collected by PINRO in the southern part of the Barents Sea (ICES area 1) for 1949-1991 (Table 1 and 2). Samples have been collected round each year, therefore mean length and weight of fish of the same age can be considered as mean-year ones.

Data, presented in Tables 1 and 2, have noticeable trends, expressed in the increase of mean length and weight from the beginning of the discussed period to its end, and caused in a great degree by changes of trawl types (Ponomarenko et al., 1985). Till 1961, trawls with 90-mm mesh size were used, in 1961-1962 - 110 mm, in 1963-1966 - 120 mm, in 1967-1980 - 130 mm for Manila rope or 120 mm for kapron and since 1981 till present time - 125 mm for kapron.

To estimate the non-uniformity of time series, the study period was divided into three sub-intervals: 1949-1966, 1967-1980 and 1981-1991. Mesh size of trawls within of each sub-period interval was conventionally accepted as constant one. Mean length and weight of cod for these sub-periods are givenin Table 3. The latter shows that mean length increased from 1949-1966 to 1981-1991 by 2-4 cm in 3-4-year fish and by 5-7 cm in 8-9-year cod, and mean weight increased by 0.1-0.2 kg in 3-4-year-olds and 1.1-1.5 kg in 8-9-year-olds.

To eliminate non-uniformity, time series were "reduced" to the last period (1981-1991). For mean lengths and weights presented in Table 3, the following designations are used: $L_{1,t}$, $L_{2,t}$, $L_{3,t}$, $W_{1,t}$, $W_{2,t}$ and $W_{3,t}$, where indices 1, 2 and 3 means periods 1949-1966, 1967-1980 and 1981-1991, correspondingly, and t - age of cod (t = 3, ..., 9). Now, we calculate differences $difL1_t = L_{3,t} - L_{1,t}$, $difL2_t = L_{3,t} - L_{2,t}$, $difW1_t = W_{3,t} - W_{1,t}$ and $difW2_t = W_{3,t} - W_{2,t}$. We mark initial length and weight of cod (Tables 1 and 2) as $L_{t,i}$ and $W_{t,i}$, where i means years (i = 1949, ..., 1991). We reduced length and weight for the period of 1949-1966 to last period (1981-1991) by formulae $LR_{t,i} = difL1_t + L_{t,i}$ and $WR_{t,i} = difW1_t + W_{t,i}$, where $LR_{t,i}$ and $WR_{t,i}$ - reduced length and weight of cod (i = 1949, ..., 1966). Data for 1967-1980 were reducted the same way with the use of formilae $LR_{t,i} = difL2_t + L_{t,i}$ и $WR_{t,i} = difW2_t + W_{t,i}$ (i = 1967, ..., 1980). As a result, mean length and weight of cod at the same age became identical for all three sub-periods and equal to mean length and weight for the period of 1981-1993. The reduced data are presented in Figs. 1a and 1b.

Mean yearly water temperature in the 0-200 m layer on the Kola section was used as an index of temperature conditions in the southern Barents Sea. Year-to-year changes of temperature are presented in Fig. 1c.

Indices characterizing food supply variations were presented by only two main components of feeding: capelin and euphausiids. A portion of 3- and 4-year capelin is great in cod diet (Ushakov et al., 1992). Two indices of capelin abundance are used. In one case, 3- and 4-year capelin abundance was divided by cod total biomass; in the second case, it was divided by biomass of cod fed on capelin during a year (Table 4). Capelin abundance of each age group was calculated as mean arithmetical of year-class abundances estimated by results of two contiguous acoustic surveys, including autumn and spring catches (Anon., 1989). Data on biomass of cod are taken from materials of the ICES Arctic Fisheries Working Group (Anon., 1993). Euphausids abundance indices are taken from Drobysheva (1988).

In addition, data for 1953-1991 reflecting per cent of cod, in stomachs of which capelin, shrimp, euphausids and young cod and redfish were occurred (or frequency of occurrence), are analyzed.

Correlational and regression analyses were used as principal methods of investigations. Periodogram analysis was used to derive quasi-cycling components. The obtained results were estimated and interpreted in acccordance with recommendations of Ferster and Rents (1983) and Afifi and Eizen (1982).

RESULTS AND DISCUSSION

Varyability of growth indices is typical for Arcto-Norwegian cod. Range between maximum and minimum mean lengths varies from 7.7 cm in 5-year-olds to 15.3 cm in 9-year-olds (Table 5). As for weight, this index increases from 0.46 kg in 3-year-fish to 3.49 kg in 9-year-fish. Standard deviations of length decrease with the increase of cod age (they are minimal in 5-6-year fish) and increase again to maximum in 9-year-olds. Standard deviations of weight increase from 0.10 kg in 3-year-fish to 0.66 kg in 9-year-fish. Distribution of mean length and weight of cod of all groups under study is close to normal. Skewness and kurtosis coefficients prove that.

In year-to-year variations of length and weight of cod of all age groups, there is a considerable conjugation. 1-2-year lag of extremes (maxima and minima) is observed for recent 20 years in older fish to compare with younger age groups (Fig. 1). Coefficients of correlation between cod lengths were found to be quite high, especially in adjoining age groups ($r = 0.76 - 0.83$, $n = 43$, $p < 0.001$). Weight changes of adjoining age groups are well correlated ($r = 0.46 - 0.84$, $n = 43$, $p < 0.01$). It justifies on the same reason, or a group of reasons, of analogous year-to-year variations of mean length and weight not only in adjoining age groups, but in a population in general. Dementeva (1976) mentioned this fact earlier.

Year-to-year variations of cod lengths and weights prove the existence of quasi-cycling components. After preliminary filtration of long-term (trend) components, the harmonic analysis has shown that fluctuations of 11-14-year and 6-8-year periods are typical for lengths and weights of all cod age groups (Table 6). A joint contribution of mentioned fluctuations into cod length and weight variances reaches 39-69 %. Quasi-cycling variations take place in year-to-year variations of water temperature as well, though they are less pronounced. This gives an opportunity to consider temperature as a factor influencing cod growth.
Considerable influence of water temperature on cod growth was observed by many authors, and the majority of them pointed out to the positive relation existence (Dementyeva and Mankevich, 1963; Ponomarenko et.al., 1985; Nakken and Raknes, 1987; Loeng, 1989; Nilssen et al., 1993). Since we analyse cod length and weight in a certain age, then it is logical to try to find a relation with temperature, summerized (or averaged) for several years or for a life cycle of a year-class, like Dementyeva and Mankevich (1965) did it assuming that temperature influences fish growth permanently. Sums of mean yearly temperatures for periods from 1 to 9 years, preceding a year of fish capture, were correlated with length and weight of fish. However, we did not find significant correlations between length/weight and temperatures sum for 5 and more years. For cod at the age of 3-5 years, the significant correlation exists between length/weight and temperature summerized for 2 years (length: $r = 0.38 - 0.44$, $n = 42$, $p < 0.05$; weight: $r = 0.32-0.34$, $n = 42$, $p < 0.05$). Length and weight of 6-7-year cod significantly correlate with temperature summerized for 3 years (length: $r = 0.46 - 0.55$, $n = 42$, $p < 0.01$; weight: $r = 0.39 - 0.47$, $n = 42$, $p < 0.01$). In fish at the age of 8-9, the significant correlation between length/weight and temperature exists when we use temperatures summerized for 4 years preceding fish capture (length: $r = 0.44 - 0.49$, $n = 42$, $p < 0.01$; weight: $r = 0.32 - 0.34$, $n = 42$, $p < 0.05$).

Thus, we can state, that there is a positive statistically significant relation between variations of cod length/weight and water temperature summerized of averaged for 2-4 years preceding a certain age.

According to indices of feeding for 1953-1991, great changes of main food objects are typical for cod (Fig. 2). Fluctuations of capelin occurrence frequency have 9-11-year periodicity with maxima at the beginning of decades and are in antiphase to fluctuations of euphausids occurrence frequency (Ponomarenko and Yaragina, 1978; 1979). In the 1970-ies, capelin occurrence frequency increased compared to the preceding period and composed 38.3 % in average, that is higher than long-term mean (26.1 %). Diminish of portion of cod fed on capelin has been observed since 1982 in connection with the decrease of capelin stock: capelin occurrence frequency composed in average 19.2 % in the 1980-ies. In same years, a role of shrimp in cod feeding increased. Maximum of shrimp occurrence frequency was in 1981-1984 (47-55 %), after it there was a decrease to 22-34 %. In the 1980-ies, juvenile redfish became more important in cod feeding because of the appearance of rich year-classes in 1982-1983 and 1989. Till the middle of the 1960-ies, the occurrence of juvenile cod in cod stomachs constituted 5-12 %, after that there was a decrease to 0-3 %, that was caused by the year-classes abundace change (Fig. 2b). Due to our data, some increase of juvenile cod occurrence in cod feeding is observed in 1985-1987. It is also proved by calculations of food consumed by cod (Tretyak et al., 1991; Bogstad and Mehl, 1992).

Year-to-year variations of food components cause the changes of mean length and weight of cod. In 1981-1983, cod growth was observed to become slow in connection with the decrease of capelin abundance and biomass. After that, cod changed to consume other food (shrimp, juvenile redfish, uncommercial fish, euphausids, temisto), and mean length and weight increased again and reached maximum in 1984-1987 in majority of age groups. Further decrease of growth indices was observed in the end of 1980-ies and was related with poor feeding with capelin and shrimp, but at increased consumption of euphausids.

Thus, changes of cod growth rates are closely connected with abundance fluctuations of main feeding objects and first of all - of capelin. However, when main prey stocks decrease, cod change to reserves and after some period of adaptation can restore potential growth possibilities.

Capelin consuming by cod during a year (Fig. 3) has two maxima (in February-April and August-October) and two minima (in June-July and November-January). To our opinion, they are mainly caused by the measure of overlapping of two distribution areas during a year (Fig. 4). Maximum overlapping is observed in February-May, when both species are distributed in the south-western part of the sea. In June-July, large squares of distribution areas are overlapped, but capelin distribute in the 0-200-m layer, mainly, in this period and do not migrate vertically in a mass into bottom layers (Luka and Ponomarenko, 1983), being beyond the reach of cod. In August-October, species distribution areas are overlapped within the large square along the polar frontal zone. Minimal overlapping of areas are observed in November-January.

In view of the lack of long time-series of data on abundance or biomass of many feeding objects, we tried to find relationships between cod length/weight and abundance of capelin and euphausids only.

With the use of a cross-correlation analysis on the basis of data for 1973-1991, it was revealed that there is a weak but statistically significant positive relation between length/weight of cod of several age groups and capelin abundance index, accounting capelin consuming by cod. As for cod length, we have found significant relations with capelin abundance at $p = 0.05$ only in 3-4-year-olds, 6- and 8-9-year-olds at shifts from minus

1 to minus 3 years with respect to the year of capture. Significant correlations between weight and abundance of capelin are revealed in 3-year-olds and 6-9-year-olds only, but at p = 0.01-0.02, that justifies on larger influence of capelin abundance on variations of cod weight than on variation of cod length.

Statistically significant relations between cod length/weight variations and euphausids abundance fluctuations were not revealed.

We have analyzed the influence of cod biomass on variations of cod length and weight, however, no statistically significant relations were revealed.

It is well known that a larger young specimen has larger length during 1-2 consequent years. Correlation analysis has shown that there is a positive statistically significant relation ($r = 0.57 -0.70$, $n = 42$, $p < 0.001$) between fish length of the same year-classes at the age of n and n-1. Cod weight variations of the same year classes at the age of n and n-1 are also significantly correlated ($r = 0.41=0.57$, $n = 42$, $p < 0.01$). Therefore, length and weight in the preceding age determines in a great measure length and weight of cod a year later.

Water temperatures in the 0-200 m layer on the Kola section averaged for 204 years, as well as capelin abundance indices and length and weight of cod at the age of n-1 were used as independent variables when creating the multiple regression models of cod length and weight. In spite of the absence of significant correlations with cod length and weight, cod biomass and euphausids abundance averaged (smoothed) by three-year periods were also included into a set of independent variables.

To obtain multiple regression models, a stepwise variable selection procedure was used. Independent variables were included into a model at F-criterium value exceeding 4.

Because of short data time-series on capelin abundance, the calculations and creation of regressional models were done on materials for 1973-1991.

As the result, linear multiple regression equations were obtained for length and weight of cod at the age of 3-9:

$$L_n = A_n + \sum_j A_{n,j} \cdot X_j$$

$$W_n = B_n + \sum_j B_{n,j} \cdot X_j$$

where L_n and W_n - length and weight of cod at the age of n years (n = 3, ..., 9);
A_{nj} and B_{nj} - coefficients of regression;
X_j - independent variables: water temperatures (mean yearly and averaged for 2-4 years), capelin abundance indices, length and weight of cod at the age of n-1, cod biomass and euphausids abundance (j = 1,....., 7); X_j = 0 if j-variable is not included into the equation;
A_n and B_n - constants.

Determination coefficients (R^2) of these equations vary from 0.66 to 0.92 (Table 7). It means that independent variables included into models explain from 66 to 92 % of cod length and weight variances. Mean standard errors (S) of the regression equations for length vary from 0.95 cm to 2.83 cm and for weight - from 0.05 kg to 0.51 kg. To estimate the quality of obtained equations, criterium (S/o) - the ratio between standard error of the regression equation and standard deviation of the dependent variable - was used. The closer a value of this ratio to zero, the better regressional dependence describes variations of the dependent variable. Regressional models, we have obtained, satisfactorily describes year-to-year variations of cod length and weight (Figs. 5 and 6). It is seen by relatively small values of ratio S/o (Table 7). Only equation for length of cod at the age of 9 is the exclusion.

Thus, year-to-year variations of cod length and weight are caused by the combined influence of big number of factors. The main of them to our opinion are water temperatures and feeding conditions. The role of some food objects can change greatly. At large decreases of capelin biomass (the main cod food object), cod begin to consume other objects. Such transitions require some time for adaptation and are accompanied by the decrease of growth rate.

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Table 1. Mean length of Arcto-Norwegian cod at different ages from ICES area 1, cm

Year	Age, years						
	3	4	5	6	7	8	9
1949	36.3	41.0	48.8	56.8	65.8	75.8	81.7
1950	37.8	43.1	48.7	56.1	64.4	75.6	82.7
1951	35.2	42.8	50.1	58.7	65.8	75.7	83.0
1952	37.8	44.1	50.3	59.9	67.1	76.0	81.6
1953	34.2	41.5	50.4	60.6	68.9	77.8	86.2
1954	38.8	45.1	53.0	62.5	72.1	80.2	85.7
1955	33.7	43.5	50.5	59.6	69.7	78.9	86.0
1956	37.8	45.5	51.8	59.8	69.3	79.5	86.8
1957	37.0	44.7	52.5	61.7	68.7	78.0	86.8
1958	40.5	45.5	51.7	61.1	69.5	76.9	82.3
1959	38.9	46.3	51.9	60.1	67.6	76.2	83.6
1960	38.4	46.2	53.6	61.7	69.8	77.0	85.2
1961	38.2	44.3	53.6	62.1	71.5	77.6	83.8
1962	39.9	45.5	51.2	61.4	70.7	79.7	84.3
1963	40.3	45.5	51.8	60.0	69.7	78.9	89.2
1964	38.6	44.2	49.6	59.9	71.0	81.5	88.6
1965	37.0	45.0	51.2	59.9	69.6	79.5	90.5
1966	41.1	46.6	53.4	60.6	67.7	76.2	84.2
1967	39.1	48.7	57.3	65.0	71.8	77.7	83.7
1968	39.4	46.3	54.2	62.4	69.6	77.0	83.8
1969	41.2	46.7	52.9	61.0	69.9	77.6	84.1
1970	39.8	46.1	55.3	60.3	68.6	76.8	83.2
1971	41.3	49.2	56.1	62.7	71.1	77.8	84.8
1972	42.3	48.8	56.0	64.5	70.4	80.1	86.5
1973	38.1	44.7	55.9	63.0	72.0	78.9	90.6
1974	36.6	43.4	51.6	60.8	71.5	76.7	84.5
1975	39.5	44.8	53.2	60.8	68.3	77.4	84.0
1976	38.7	45.2	53.0	61.1	69.5	77.3	83.4
1977	38.4	45.9	53.9	61.4	70.2	79.1	86.8
1978	38.0	44.9	55.1	62.3	69.9	77.1	83.8
1979	34.9	42.6	52.0	61.1	70.2	77.2	83.4
1980	36.3	43.8	52.2	60.9	69.2	78.3	86.8
1981	40.4	47.0	52.7	60.6	71.2	80.5	87.2
1982	41.2	46.6	56.3	62.7	70.8	78.4	84.7
1983	42.9	51.8	59.9	67.3	74.0	80.1	92.6
1984	43.3	51.5	60.4	69.4	77.9	83.4	92.1
1985	44.6	52.4	58.7	68.2	78.2	86.1	90.2
1986	41.8	50.7	58.5	65.1	77.1	87.9	95.7
1987	35.1	48.6	57.5	67.2	76.1	90.1	100.0
1988	37.2	44.7	53.6	63.9	75.3	87.5	99.5
1989	36.8	46.2	52.7	60.0	67.9	76.9	88.4
1990	41.3	53.6	59.6	63.7	72.0	79.1	91.2
1991	45.2	53.5	60.1	67.5	75.5	81.4	94.0

Table 2. Mean weight of Arcto-Norwegian cod at different ages from ICES area 1, kg

Year	Age, years						
	3	4	5	6	7	8	9
1949	0.575	0.650	1.127	1.740	2.480	3.717	5.542
1950	0.530	0.890	1.150	1.551	2.342	3.764	4.922
1951	0.388	0.722	1.039	1.806	2.407	3.726	4.867
1952	0.458	0.783	1.141	1.969	2.594	3.750	4.849
1953	0.362	0.635	1.136	1.901	2.735	4.015	6.720
1954	0.553	0.829	1.274	2.301	3.234	3.780	6.471
1955	0.361	0.759	1.173	1.891	2.977	3.856	5.214
1956	0.517	0.836	1.081	1.795	2.716	4.029	5.366
1957	0.451	0.849	1.301	2.019	2.754	4.038	5.774
1958	0.594	0.825	1.200	2.052	2.967	3.868	4.700
1959	0.556	0.942	1.304	1.940	2.723	3.885	5.088
1960	0.544	0.929	1.420	2.079	3.074	4.055	5.757
1961	0.546	0.815	1.385	2.128	3.238	4.059	5.006
1962	0.590	0.880	1.231	1.976	2.963	4.140	5.203
1963	0.588	0.830	1.178	1.795	2.780	3.949	5.687
1964	0.499	0.706	0.985	1.730	2.822	4.495	5.484
1965	0.537	0.816	1.159	1.768	2.757	3.947	6.003
1966	0.631	0.916	1.409	1.931	2.658	3.888	5.481
1967	0.536	1.000	1.552	2.293	3.192	4.090	5.317
1968	0.488	0.792	1.315	2.005	2.791	3.889	5.090
1969	0.585	0.876	1.228	1.823	2.789	3.914	5.006
1970	0.565	0.888	1.334	1.927	2.824	4.008	5.234
1971	0.647	1.107	1.607	2.230	3.236	4.226	5.554
1972	0.708	1.021	1.532	2.364	3.142	4.728	6.111
1973	0.468	0.751	1.459	2.071	3.103	4.365	6.223
1974	0.423	0.703	1.168	1.897	3.132	3.913	5.213
1975	0.552	0.796	1.327	1.923	2.938	4.274	5.223
1976	0.530	0.834	1.359	2.100	3.020	4.244	5.630
1977	0.506	0.879	1.381	2.023	2.927	4.361	5.793
1978	0.479	0.777	1.425	2.040	2.818	3.832	5.200
1979	0.363	0.662	1.171	1.884	2.927	3.766	4.903
1980	0.457	0.768	1.239	1.929	2.843	4.080	5.759
1981	0.570	0.911	1.332	2.033	3.084	4.794	5.923
1982	0.628	0.928	1.602	2.164	3.101	4.046	5.452
1983	0.769	1.321	2.005	2.750	3.772	4.762	7.794
1984	0.749	1.242	1.917	2.779	3.970	5.185	7.443
1985	0.772	1.224	1.731	2.693	4.000	5.418	6.374
1986	0.632	1.112	1.680	2.305	3.885	5.946	7.607
1987	0.335	0.976	1.551	2.302	3.285	6.444	8.233
1988	0.476	0.825	1.373	2.228	3.558	6.385	8.943
1989	0.482	0.911	1.308	1.919	2.730	4.125	6.541
1990	0.683	1.439	1.949	2.261	3.262	4.224	6.516
1991	0.644	0.981	1.618	2.375	3.186	4.245	6.643

Table 3. Mean length (cm) and weight (kg) of cod calculated for periods with relatively constant mesh size of trawls

Period, years	No. of years	Age, years						
		3	4	5	6	7	8	9
					Length			
1949-1966	18	37.9	44.5	51.3	60.1	68.8	77.8	85.1
1967-1980	14	38.8	45.8	54.0	62.0	70.2	77.8	85.0
1981-1991	11	40.6	49.1	56.9	64.7	73.9	82.7	92.0
					Weight			
1949-1966	18	0.52	0.81	1.20	1.91	2.79	3.94	5.45
1967-1980	14	0.52	0.85	1.36	2.04	2.98	4.12	5.45
1981-1991	11	0.61	1.08	1.64	2.34	3.44	5.05	7.04

Table 4. Abundance indices of capelin and euphausids, and biomass of cod

Year	Capelin abundance idex		Cod biomass, thou. tons	Euphausids abundance, spec./thou. m^3
	relative to total cod biomass, 10^9 spec/thou. tons	relative to biomass of cod fed on capelin, 10^9 spec/thou. tons		
1962	-	-	2900	521
1963	-	-	2513	-
1964	-	-	1966	128
1965	-	-	2190	87
1966	-	-	3026	179
1967	-	-	3855	108
1968	-	-	3978	111
1969	-	-	3417	322
1970	-	-	2423	334
1971	-	-	1866	248
1972	-	-	2048	970
1973	0.110	0.291	2966	241
1974	0.129	0.212	3066	152
1975	0.293	0.504	2734	2269
1976	0.266	0.514	2511	232
1977	0.236	0.444	2146	412
1978	0.230	0.611	1794	136
1979	0.398	0.919	1387	481
1980	0.446	0.927	1237	718
1981	0.362	0.700	1085	556
1982	0.342	1.072	938	674
1983	0.466	1.327	760	190
1984	0.249	1.547	908	315
1985	0.159	3.228	1008	147
1986	0.033	0.184	1296	1275
1987	0.003	0.053	1129	553
1988	0.001	0.012	833	668
1989	0.017	0.126	934	270
1990	0.023	0.122	1084	195
1991	0.107	0.496	1663	49

Table 5. Summary statistics for "reduced" data on mean length and weight of cod at age 3-9 from ICES area 1.

Statistics	Age, years						
	3	4	5	6	7	8	9
				Length, cm			
No. of years	43	43	43	43	43	43	43
Mean	40.59	49.08	56.90	64.71	73.89	82.71	91.99
Median	40.90	49.20	56.80	64.50	74.00	82.50	91.20
Minimum	35.10	44.70	52.70	60.00	67.90	76.90	84.70
Maximum	44.60	53.60	60.40	69.40	78.20	90.10	100.00
Stand. dev.	2.26	2.12	1.97	1.99	2.19	2.53	3.08
Skewness	-0.52	0.02	-0.22	-0.13	-0.36	0.57	0.64
Kurtosis	-0.22	-0.63	-0.50	0.42	0.35	1.16	0.96
				Weight, kg			
No. of years	43	43	43	43	43	43	43
Mean	0.61	1.08	1.64	2.35	3.44	5.05	7.04
Median	0.63	1.08	1.62	2.33	3.40	5.01	6.91
Minimum	0.34	0.83	1.31	1.92	2.73	4.05	5.45
Maximum	0.80	1.44	2.01	2.78	4.00	6.44	8.94
Stand. dev.	0.10	0.13	0.16	0.20	0.28	0.48	0.66
Skewness	-0.50	0.49	0.16	0.40	0.03	0.73	0.50
Kurtosis	0.40	0.13	-0.19	0.04	0.04	2.38	0.95

Table 6. Contribution (%) of fluctuations with different periods into cod length and weight variances.

Period, years	Age, years 3	4	5	6	7	8	9
			Length				
42.0	1	3	0	1	2	3	3
21.0	6	9	2	4	9	10	5
14.0	11	23	28	32	25	12	11
10.5	15	4	5	14	27	28	28
8.4	13	10	12	11	6	10	7
7.0	11	8	2	0	1	6	4
6.0	2	7	18	10	7	5	2
5.3	0	1	5	7	0	4	0
4.7	10	8	5	2	2	6	12
4.2	0	1	1	2	0	0	1
3.8	2	4	5	5	3	6	4
3.5	0	2	0	0	2	1	7
3.2	2	2	4	3	5	2	4
3.0	3	6	5	4	3	1	4
2.8	2	0	1	1	1	0	2
2.6	1	1	1	2	1	3	0
2.5	2	0	2	0	1	0	0
2.3	0	2	0	0	3	1	4
2.2	1	3	0	1	0	0	1
2.1	7	5	4	0	3	1	1
2.0	10	1	0	0	0	0	0
				Weight			
42.0	0	2	0	0	1	3	4
21.0	8	6	2	3	7	9	6
14.0	6	15	18	31	31	19	9
10.5	16	7	9	12	22	16	19
8.4	13	11	14	9	5	6	4
7.0	16	10	4	0	1	7	2
6.0	8	11	23	17	10	5	5
5.3	1	2	4	4	0	9	2
4.7	8	6	5	5	1	3	4
4.2	0	1	2	3	2	1	3
3.8	0	3	3	2	1	9	20
3.5	0	2	1	0	1	5	7
3.2	3	2	2	4	4	2	1
3.0	1	7	3	3	3	1	3
2.8	3	0	0	1	1	0	0
2.6	3	1	0	3	1	2	5
2.5	2	1	2	0	1	0	2
2.3	0	5	2	1	5	2	2
2.2	2	4	1	2	0	2	1
2.1	4	6	3	0	4	1	0
2.0	6	1	0	0	0	0	0

Table 7. Determination coefficients (R^2), standard errors (S) and ratios S/σ for cod length and weight regression models

Parameter	Age, years						
	3	4	5	6	7	8	9
				Length, cm			
R^2	0.92	0.88	0.84	0.89	0.92	0.83	0.66
S	0.95	1.10	1.26	1.02	0.95	1.95	2.83
S/σ	0.35	0.41	0.53	0.43	0.36	0.56	0.70
				Weight, kg			
R^2	0.81	0.85	0.90	0.88	0.86	0.86	0.81
S	0.05	0.05	0.06	0.09	0.14	0.32	0.51
S/σ	0.49	0.42	0.38	0.43	0.47	0.49	0.65

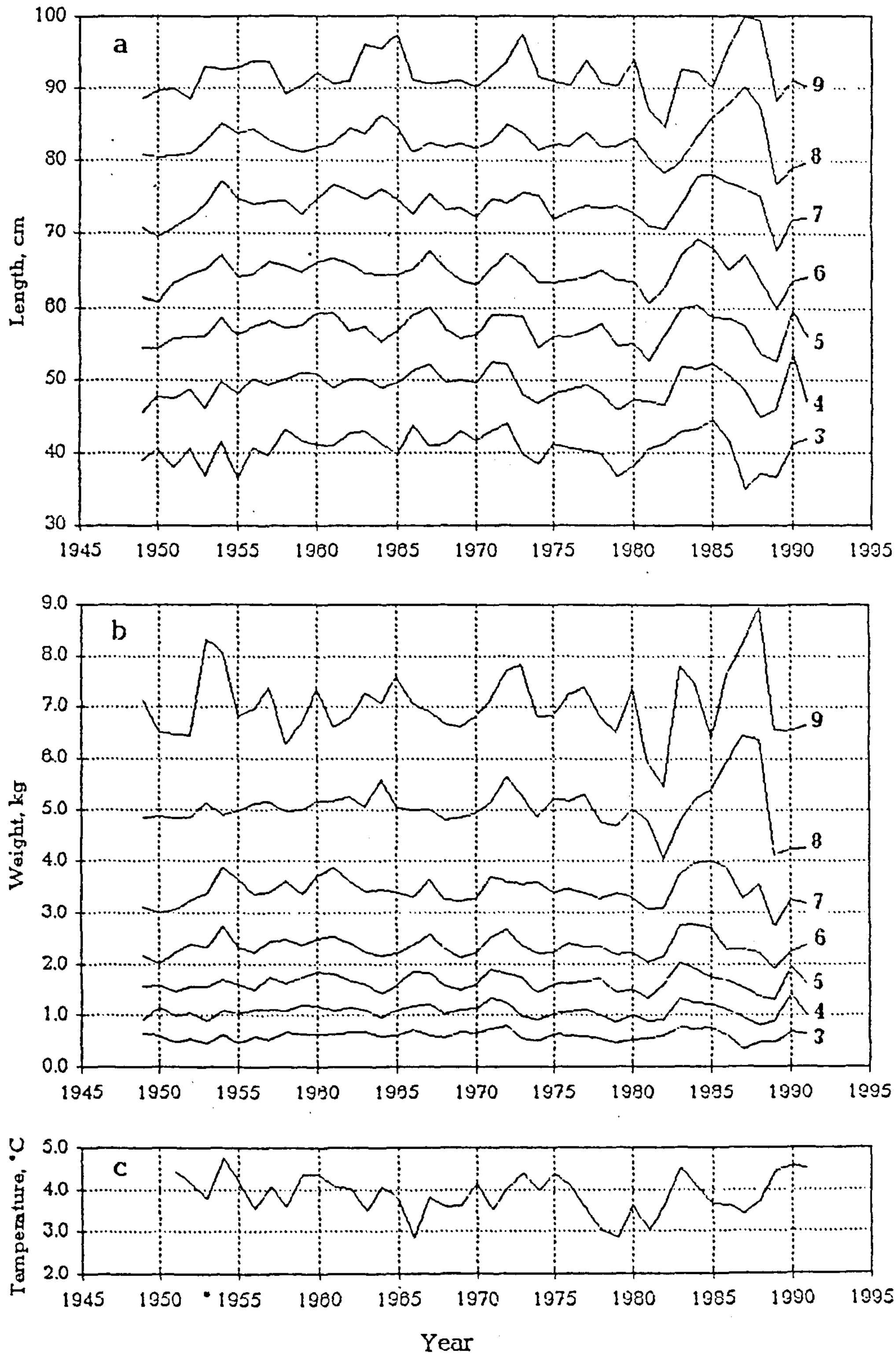

Fig. 1. Year-to-year variations of mean lengths (a) and weights (b) of cod at the age of 3-9 as well as water temperatures for 0-200 m layer in the Kola section (c).

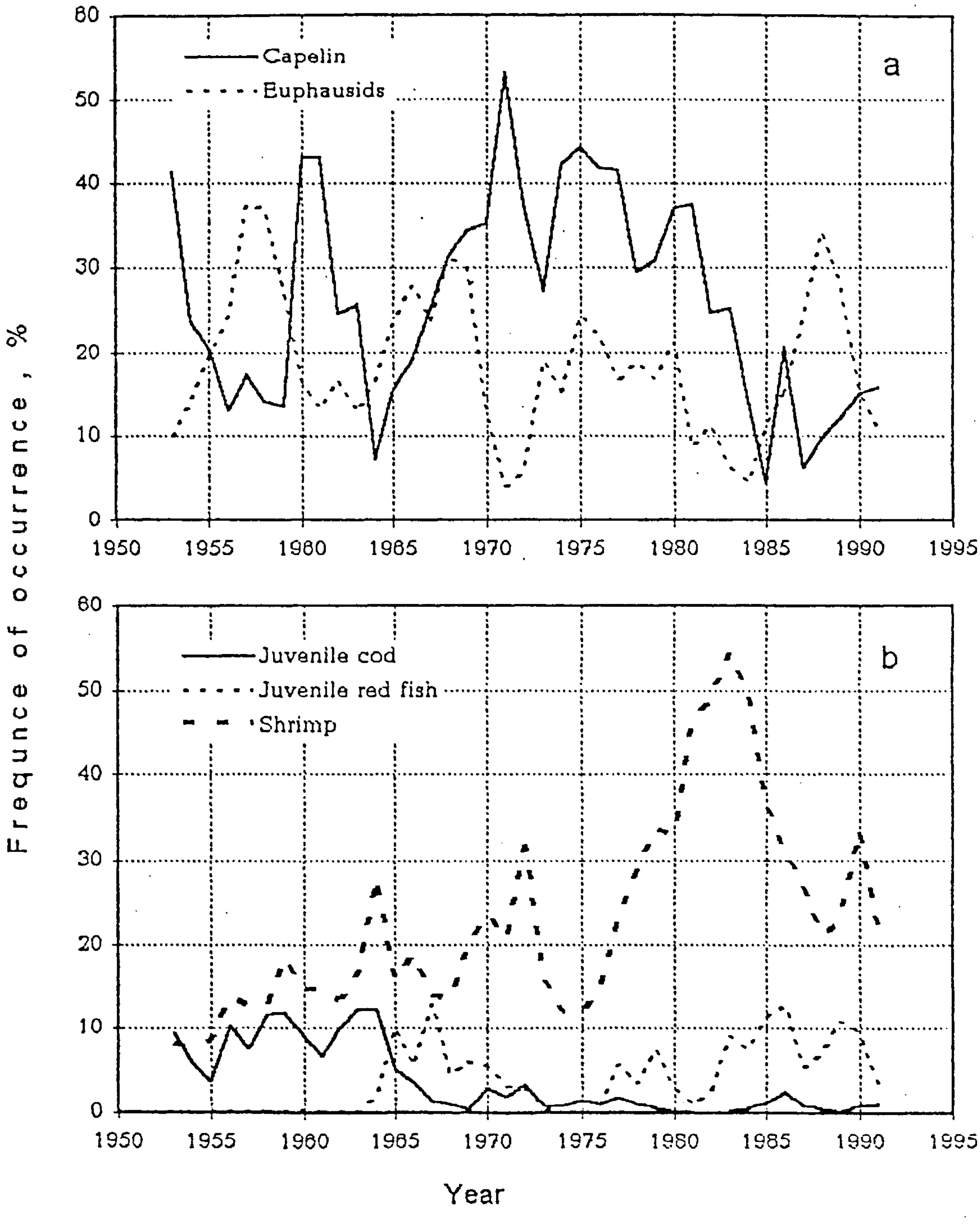

Fig. 2. Year-to-year variations of occurrence frecuences (%) of capelin and euphausiids (a); shrimp, young cod and young redfish (b) in cod stomachs.

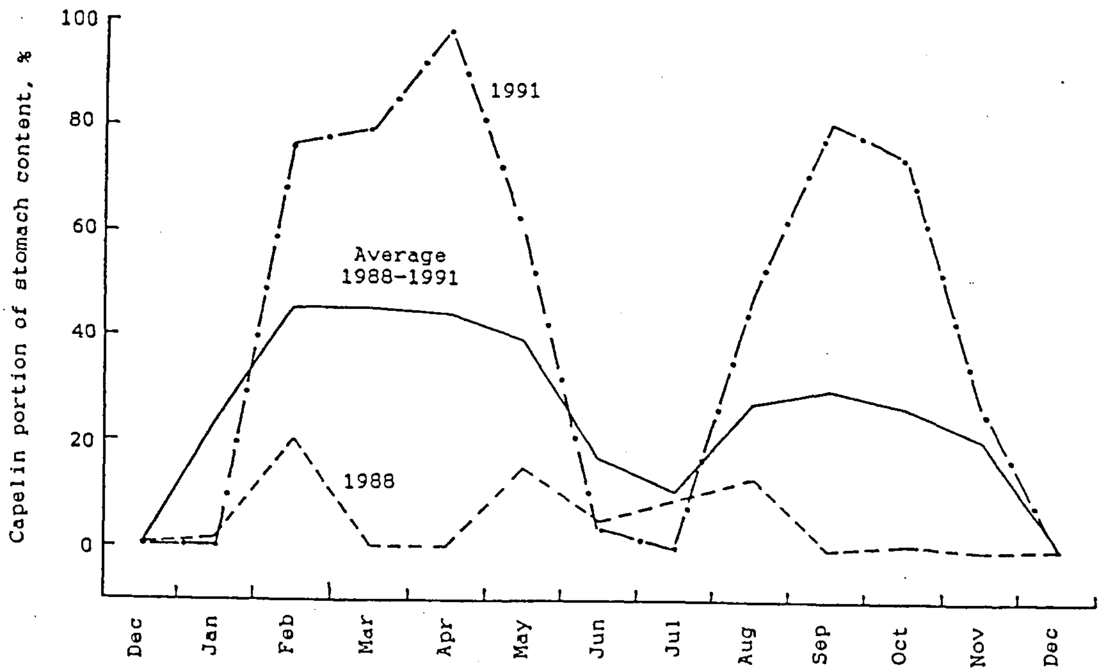

Fig. 3. Seasonal variations of capelin portion in a mass of cod nutritional bolus in 1988-1991, %.

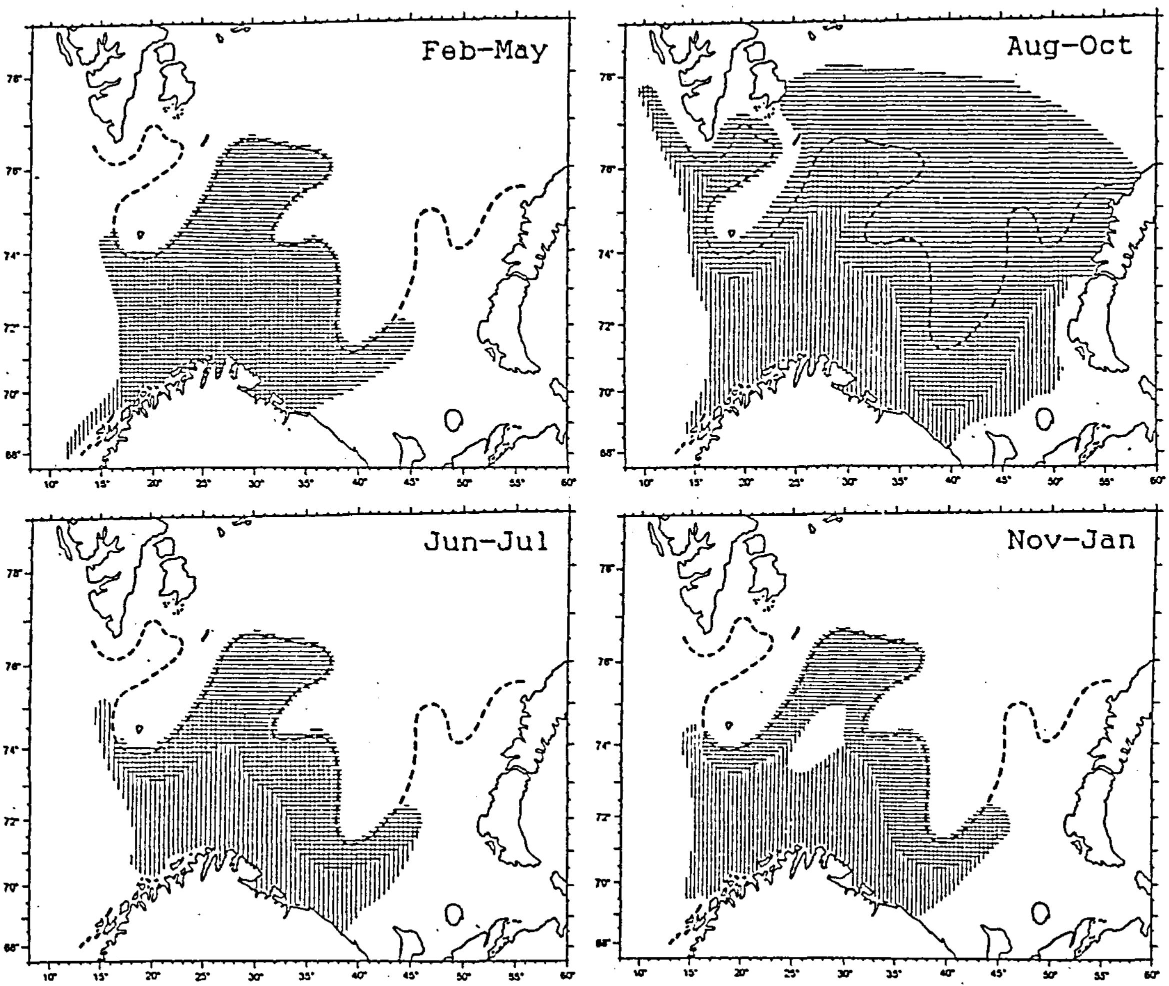

Fig. 4. Distribution of cod (vertical shading) and capelin (horizontal shading) in different periods of a year.

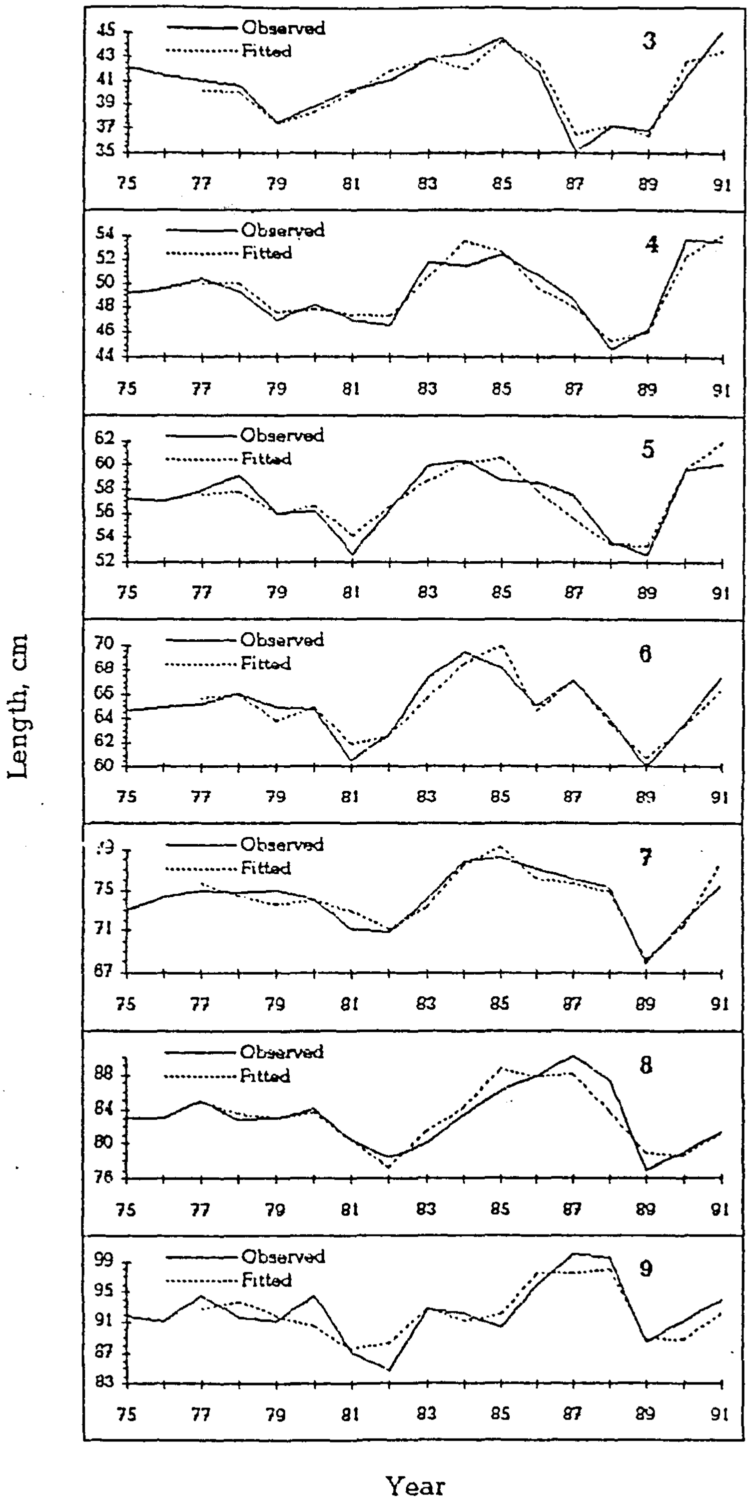

Fig. 5. Actual and calculated by a model length of cod at the age of 3-9.

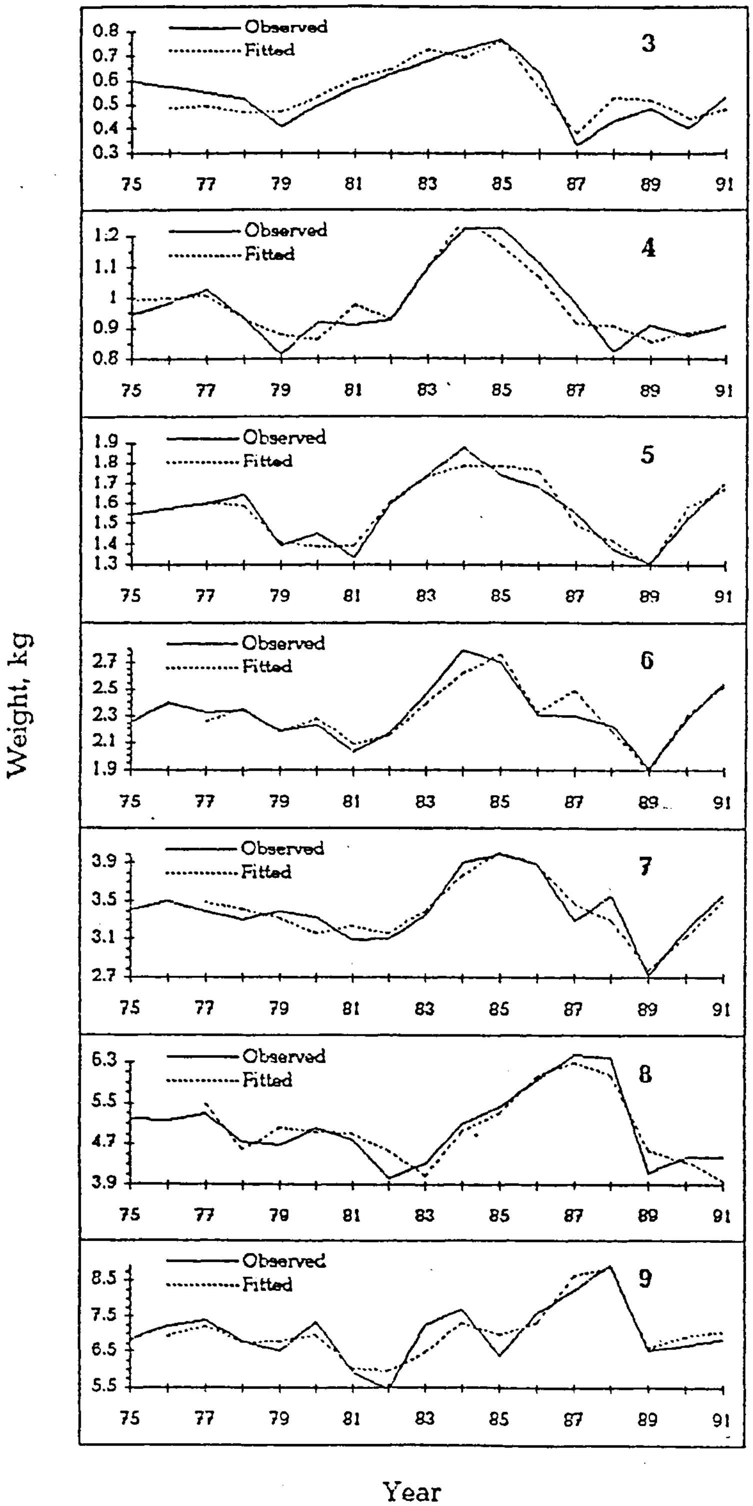

Fig. 6. Actual and calculated by a model weight of cod at the age of 3-9.