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Can a Bioenergetics Model Explain Growth Of The Northeast Arctic Cod?

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ABSTRACT

For the period 1984 to 1991, the individual maximum daily consumption in calories (C_{max}) based on 33000 cod stomach samples is given by the power equation:

$$C_{max} = 68.84 \cdot W^{0.934}$$

where W represents the total fish weight in grams. Daily consumption as proportion of individual maximum consumption, laboratory determination of metabolism, specific dynamic action, activity multiplier and spawning losses were incorporated into a bioenergetics model to predict growth in energy value for the Northeast Arctic Cod. Results based on 1990 data indicated that the amount of assimilated energy (90% of actual fraction of the maximum consumption) allocated for each components varied according to the season. Highest food conversion efficiency occurred during the first half of 1990 and declined during the second half. The annual rates of food turnover were within 20% — 27% of the annual consumption. Comparisons were made between four cod stocks concerning the annual energy requirements.

INTRODUCTION

Bioenergetic models offer an alternative approach for estimating consumption in combination with field data on fish growth and water temperature (Niimi and Beamish, 1974; Majkowski and Waiwood, 1981;Rice and Cochran, 1984; Jobling, 1988; Hewett and Johnson, 1989). The usefulness of these models in evaluating food demand depends in part on the availability and quality of information necessary to drive model parameters (Bartell et al. 1986). In addition, Bartell et al (1986) cited that the above approach is more reliable than the estimation of growth from a given consumption.

A potential problem with this approach (consumption from given growth) is that the coefficients of variation of weight at age for the Barents Sea cod is very high and generally larger than in the North Sea and the Baltic Sea cod. This is mainly caused by a discrepancy in age reading, sampling and fish migration. Application of the above approach would result in a greater variability in the daily ration for each age group than actually occurs in the natural environment.

One of the several recommendations suggested by "The Nordic workshop on bioenergetics of fish at Tovetorp in 1991" is that the Wisconsin type model gave consumption estimates that were comparable to independent estimates from gastric evacuation models, and at present cannot be rejected as a possible method for estimating consumption (Anon. 1991b). Therefore, the bioenergetic model has been developed here in a form so that the individual field consumption as proportion of maximum consumption is the available input data, and the individual growth is the desired output.

MATERIALS

STOMACH DATA

A total of 33000 cod stomachs were collected by the Norwegian research vessels from 1984 to 1991 during routine surveys in the Barents Sea. The Barents Sea was covered mainly from the end of January until the beginning of March, from the end of April until the beginning of June, and from the beginning of September until the beginning of November (Mehl, 1989). The stomach data were aggregated by individual predator, year, season, area, length, weight, age, maturity and prey items as the first input data to the model.

TEMPERATURE

The temperature is calculated by the temperature model which is used by the multispecies model for the Barents Sea (MULTSPEC). Following the definition of a temperature file by position, year, month, depth and time of the day, the temperature program adds a temperature value for each observation. The results of combining the stomachs and temperature data were written into a new data file.

METHODS

CONSUMPTION

The daily consumption in grams of the major prey items in cod stomach is estimated for individual fish by the following (dos Santos, 1990):

$$C_i = \frac{24 \cdot w_i \cdot \ln(2) \cdot \left(\frac{st}{w_f \cdot 1000}\right)^{0.54}}{H_i \cdot e^{-T \cdot 0.11}} \qquad 1$$

where H_i=205 (krill), 533 (shrimp), 452 (herring, red fish), 283 (capelin) and 368 (other food), st=mean stomach weight, w_f=fish weight in Kg, T=temperature °C and w_i=mean weight of prey (i) in cod stomachs.

Following the calculation of the consumption of all preys in the stomach, the consumption of each prey is multiplied by the average caloric density of the prey, and finally summed to give a consumption per day in calories for each individual fish.

MAXIMUM CONSUMPTION

The maximum amount of food available for growth and other activities of cod have been investigated by Jobling (1988), and the studies were carried out at temperatures within the range 7–11 °C using cod 100–700g in weight. Caution should be exercised in applying Jobling's formula for the Barents Sea cod Stock. This is simply because (1) cod can be found below the experimental temperature and (2) the fish weight range used in that study represented only one to two years old cod in the Barents Sea. Alternatively, we assume that there is a theoretical line representing a possible maximum consumption per day based on a relationship between individual consumption in calories and fish weight.. This relationship is shown in Fig.1. Estimated regression parameters were run by SAS procedure and the relationship was described as:

$$C_{max}(cal/day) = 68.84 * W^{0.934} \tag{2}$$

Where C_{max} is defined as maximum consumption in calories per day and W fish weight in grams.

MODEL DESCRIPTION

Based on the approach described by Hewett and Johnson (1989), the consumption is balanced by growth, reproduction, metabolism and waste products. The daily consumption (cal/day) in our approach is estimated directly as a proportion of a possible maximum consumption at any weight:

$$C_d = C_{max} \cdot P \tag{3}$$

In general, the bioenergetic model can be expressed as:

$$\frac{\Delta w}{\Delta t} = C_d(1 - f - u) - M - S_l \tag{4}$$

with:

C_d— daily consumption in calories

f — energy egested (faces)

u — energy excreted (ammonia and urea)

M — total metabolism

S_l— spawning losses

In which C_d is calculated as:

$$C_d = P \cdot a_1 \cdot W^{b1} \tag{5}$$

where P —fraction of the maximum consumption.

The total metabolism (M) can be split into :

$$M = m_s + m_d + m_a \tag{6}$$

where m_s is the standard metabolism, m_d is a specific dynamic action and m_a is the active metabolism.

The standard metabolism (m_s) is a function of fish body weight and temperature:

$$m_s = a_2 \cdot W^{b2} \cdot e^{mT} \qquad 7$$

The specific dynamic action (SDA) is a metabolic component related to the energy requirement for ingestion, digestion and absorption of the food, and its maximum rate appears to be approximately double the standard metabolism for most of the fish species (Jobling, 1981).

The spawning losses (S_l) which is the daily energetic cost of reproductive growth for mature fish, can be estimated as:

$$S_l = a_3 \cdot L^{b_3} \cdot E_w \cdot C_g/180 \qquad 8$$

where L — total fish length (cm), E_w is the wet weight in gram of one egg and C_g is the caloric density of one gram ovary. Table 1 summarizes parameter values applied, together with sources.

Table 1. Parameter values and sources.

Parameters	Sources
a_2=0.16	Karamushko(1989)
b_2=0.7834	=
m=0.0723	=
a_3=1.25*10**-2	Kjesbu (1988)
b_3=4.27	=
E_w=0.00164	Kjesbu (pers.comm.)
C_g=1000	Jobling (1982)
m_d=1.38 (max daily ration=2%)	Karamushko (1989)
=1.55(max daily ration=4%)	=
=1.94(max daily ration=6%)	=
caloric density of capelin=1670	Jobling (1982)
caloric density of shrimp=1060	=
caloric density of krill=930	=
caloric density of herring=1362	Daan (1975)
caloric density of red fish(lean fish)=1000	Nordic workshop (1991)
caloric density of zooplankton=1000	=

ACTIVITY METABOLISM

Activity metabolism is the most difficult parameter to estimates in field condition. In general, doubling of the standard rate of metabolism is a useful approximation of the activity metabolism of a fish which optimizes its growth rate in nature (Mann, 1978). Our approximation of the activity is based on the following:

total metabolism = assimilation — growth, then

activity = total metabolism — (SDA+standard metabolism).

Growth data were obtained by fitting a regression line to the observed weight for each age group during 1990. Growth increment for age 2 amounted 0.598 gr/day, 1.702 gr/day, 1.616 gr/day, 3.049 gr/day and 2.788 gr/day for age 3, 4, 5 and 6 years, respectively. The following text table shows the activity multiplier by age and quarter.

Fish age	Quarter 1	Quarter 2	Quarter 3	Quarter 4
2	1.0	1.0	1.0	1.08
3	1.50	1.0	1.0	1.0
4	2.35	1.0	1.0	1.47
5	1.6	1.0	1.0	1.7
6	2.96	1.02	1.02	1.72

The bioenergetics model programs were written in SAS by the senior author. From the user menu, one can select the following: (1) results of the model output in calories or in percent of the body weight, (2) data (from 1984 to 1991), (3) cod age or length interval , (4) fraction of the maximum consumption, (5) activity multiplier, (6) quarter or all and (7) area according to multispecies area division or all areas. According to the menu, the bioenergetic model would compute for each age group the energy requirement for each component of the energetic equation and would estimates the food conversion efficiency per day on an individual basis. The text table below shows the actual fraction of the maximum consumption (actual consumption in cal / maximum consumption) by age and quarter during 1990, numbers of observation are given in parenthesis.

Age	Quarter1	Quarter2	Quarter3	Quarter4
2	0.241(260)	0.125 (58)	0.212 (113)	0.346 (30)
3	0.317 (201)	0.114 (66)	0.184 (95)	0.180(52)
4	0.335 (231)	0.140 (64)	0.221(146)	0.211 (18)
5	0.271 (225)	0.122 (68)	0.241(150)	0.252(21)
6	0.376 (149)	0.194(55)	0.227 (133)	0.047(10)

RESULTS

SEASONAL GROWTH

The stomachs data for 1990 were selected for growth analysis. Food conversion efficiency (weight gain in calories / 90% fraction of the maximum consumption) per day was estimated for each age group based on the following assumptions: Northeast Arctic cod daily consumption in calories equal to the fraction of the maximum consumption and activity multiplier was set according to the text table above. Results of the simulation is shown in Table 2. The growth efficiency ranged from 9.6% for cod at age 2 years in autumn to 33% for cod at age 6 years in the second quarter. Based on a comparison of efficiency for each age group by season, it appears that the highest food conversion efficiency occurred either during the first or the second quarter for all age groups, except age 4 due to low number of observation(only 18 during 4th quarter), and declined during the last quarter of the year. There is no clear trend in the food conversion efficiency for the predicted growth with increasing fish age.

Table 2. Estimates of the daily energy requirements in calories by age group during 1990 (average of individual), Q-quarter and T-temperature.

Fish age	Q	T °C	P value	Growth cal/day	St.metabolism cal/day	S.D.A. cal/day	Consumption cal/day	Food efficiency % ± std dev
2	1	3.61	0.24	761	1153	438	2616	29(8.8)
	2	3.41	0.20	558	1373	522	2727	20(9.2)
	3	3.23	0.20	763	1580	600	3411	22(7.3)
	4	4.91	0.21	753	2175	826	7074	9.6(17.7)
3	1	4.18	0.31	2405	2435	925	7760	32.8(7.6)
	2	3.64	0.20	1098	2171	825	4550	25.8(7.3)
	3	3.29	0.20	1408	2892	1099	6000	23.8(7.8)
	4	5.09	0.18	1114	3924	1491	7256	15.4((15)
4	1	4.25	0.33	2154	3764	1430	13814	15.7(7.2)
	2	3.95	0.20	2293	3529	1341	7959	31(7.4)
	3	2.94	0.20	2704	4068	1545	11367	24(9.2)
	4	3.77	0.22	3974	5218	1983	13403	32(9.1)
5	1	4.33	0.27	4507	5170	1964	16384	29.5(5.4)
	2	3.84	0.16	1971	5255	1996	10248	21(6.8)
	3	2.84	0.16	5394	6074	2308	20031	28(9.0)
	4	3.06	0.24	4361	6961	2645	23409	20(9.6)
6	1	4.51	0.37	5616	6914	2627	31903	18.9(5.4)
	2	4.42	0.19	4961	6938	2636	16306	33(7.1)
	3	2.79	0.19	6092	7408	2815	24056	26.8(9.2)
	4	3.54	0.22	1733	8425	3201	15219	12.4(10.7)

ANNUAL ENERGY REQUIREMENTS

Estimates of seasonal and the annual energy requirements of the Northeast Arctic cod, in terms of consumption, growth and total metabolism in Kcal during 1990 are shown in Table 3. The energy requirements for total metabolism, calculated as annual averages for fish of various age groups are relatively high; more than 50% of the total energy budget. The Northeast Arctic cod, however, are among slower-growing fish stock, an active migrant (northward and eastward feeding migrations) with low consumption rate, and therefore the value of the annual total metabolism seems reasonable. The bioenergetics model predicts an increase in total metabolism as a percent of the total energy budget during the fourth quarter of 1990, compared with the first quarter of the same year and for all age groups, except age 4; From 67% in age 2 during the first to 88% during the fourth quarter of the year, from 65% to 82%, from 69% to 79% and from 80% to 87% for cod at age 3, 5, and 6 years old, respectively. In terms of the annual rates of food turnover, maximum 26.6% of the annual consumption is recorded in 4 years old fish, 20% in 2, 26% in 3, 25.7% in 5 and 23.4% in 6 years.

Table 3. Quarterly and annual energy requirements in Kcal by age group during 1990.

Age	Quarter	Growth	Metabolism (standard +activity)	S.D.A	Consumption
2	1	68.49	103.77	39.42	211.90
	2	50.77	124.94	47.50	223.34
	3	70.19	156.98	55.20	282.43
	4	69.27	440.22	75.99	585.73
	Total	258.7	825.9	218.1	1303.4
3	1	216.45	328.73	83.25	628.56
	2	99.91	197.56	75.07	372.65
	3	129.53	266.06	101.10	496.80
	4	102.48	361.01	137.17	600.80
	Total	548.3	1153.3	396.6	2098.8
4	1	193.86	796.08	128.70	1118.93
	2	208.66	321.14	122.03	651.60
	3	248.77	550.16	142.14	941.19
	4	365.61	561.67	182.43	1109.77
	Total	1016.9	2229.0	575.3	3821.4

5	1	405.06	744.48	176.76	1327.10
	2	179.36	478.21	181.63	839.31
	3	496.25	949.97	212.33	1658.57
	4	401.21	1293.63	243.34	1938.27
	Total	1482.4	3466.2	814.0	5763.2
6	1	505.44	1841.89	236.43	2584.14
	2	451.45	643.99	239.88	1335.46
	3	560.46	1172.24	258.98	1991.84
	4	159.44	806.10	294.49	1260.13
	Total	1676.7	4464.2	1029.7	7171.5

In order to investigate the behaviour of the bioenergetics model, we have made several runs on a daily basis with P values varied according to season and the fish age using activity multiplier as given in (Table 2). The following mean weights (grams) at age (age2 =217, age3=399, age4=868, age5=1273 and age6=1876gr) were used as the fish mean weight at January first, assuming one gram wet weight cod has an energy content of one kcal. Simulated growth was compared with the observed growth for various age groups as shown in Figs. 2, 3, 4, 5 and 6. Cod at age 2 grew at P values (table 2) from 217 to 475 grams by December 31 of 1990, from 399 to 947 grams, from 868 to 1884 grams, from 1273 to 2755 grams and from 1876 to 3552 grams for cod at 3, 4, 5 and 6 years of age, respectively. According to the bottom trawl survey during winter 1991 in the Barents Sea (unpublished report), the following weight at age for cod was recorded: age 3 (720 gr), age 4 (1370 gr), age 5 (2040 gr), age 6 (2850 gr) and age 7 (3660 gr).

COMPARISON BETWEEN COD STOCKS

Jobling (1982) provided the annual estimates of growth, maintenance and reproduction requirements in energy value for the North Sea, Faroe and Balsfjord cod. Those data were compared with the annual energy requirements during 1990 for the immature part of the Barents Sea cod, generated by the present study using the same energy units (Table 4). Note that the consumption model and the parameter values which are used in the present paper, are different from those implemented by Jobling (1982) and is likely to have contributed to the differences between the cod stocks. However, the result of the comparison between the four cod stocks has indicated that the annual consumption of the North Sea and the Faroe cod is generally higher than that of the Balsfjord and the Barents Sea cod. As for the annual metabolism cost, the value exceeded 50% of the total energy in all age groups of the Northeast Arctic cod and at age 3, 5 and 6 years old in the Balsfjord cod.

Table 4. Annual energy requirements in Kcal of the North Sea, Faroe, Balsfjord and Northeast Arctic cod by age.

Age	Cod type	Growth	Metabolism	Consumption
2	NS	4874	2540	8299
	FC	3300	2374	6483
	BC	1421	1018	2439
	NC	259	1044	1303
3	NS	9682	5379	17438
	FC	4660	4048	10341
	BC	1431	1686	3117
	NC	548	1549	2098
4	NS	8505	8387	21158
	FC	6152	6016	14922
	BC	1908	2369	4951
	NC	1017	2804	3821
5	NS	7202	10715	23805
	FC	6401	8068	18524
	BC	1677	2989	5354
	NC	1482	4280	5763
6	NS	7058	12688	27108
	FC	6772	10046	22226
	BC	2100	3599	6835
	NC	1676	5493	7171

where NS-North Sea cod, FC-Faroe cod, BC-Balsfjord cod and NC-Northeast Arctic cod.

DISCUSSION

The closeness of the predicted growth during 1990 to the observed growth suggests that both our bioenergetic model's assumptions which are :

(1) Cod consumed from 16% to 37% of the maximum rations.

(2) Activity modeled from 1.00 to 2.96 of the standard metabolism.

(3) No spawning losses up to age 7.

(4) Unnecessary sorting cod according to sex (Smith et al., 1986).

(5) 90% assimilation efficiency, and parameter estimates represent a valid application of bioenergetic approach for the Northeast Arctic cod based on field observations. One of the surprising results of our study is that the food conversion efficiency for predicted growth is not decreasing with increasing fish age for the immature part of the Barents Sea cod (Table. 2). This is contrary to general belief that the gross food efficiency decreases with increasing fish age. Daan (1975) reported a decrease in food efficiency with increasing fish age in the North Sea cod. Steele (1965), on the other hand, reported a constant efficiency with increasing age in Herring while in Haddock the efficiency is declining with increasing age.

The maturation of the Northeast Arctic cod is delayed until age 7 (Anon, 1991a). To promote gonadal maturation, cod are totally dependent on the reserves of protein in the white muscle and fat in the liver (Kjesbu et al., 1991). This delay will lead to increase in the amount of energy available for growth for immatures compared with the mature part of the population, at similar level of activity and maintenance. Consequently, the efficiency of conversion will change towards a decline with increasing fish age, more likely at or after age 7. According to Jobling (1982), the reproductive costs amounted to about 15% of the total energy in the Balsfjord cod, 22% in the Faroe and the North Sea cod. Smith et al. (1989), however, reported that 30% to 31% of prespawning stored energy was expended during the spawning effort in the Pacific cod.

The peak in food conversion efficiency does not coincide with consumption rate during the season (Table 2). Efficiency for age 3 in winter amounted to 29% with daily consumption 2616 (cal/day) while in summer the efficiency and the consumption reached 22% and 3411 cal/day, respectively. Similar results were also found for the other age groups. The above results would suggest that increasing daily ration resulted in decreased food conversion efficiency which is caused by an increase of the specific dynamic action and activity leading to increase in the metabolic level. Further study is required to examine the relationship between feeding level and food conversion efficiency for the Northeast Arctic cod in a field situation.

Results in Table 2 indicate that the amount of assimilated energy (90% of the actual fraction of the maximum consumption) allocated for metabolism and growth varied according to the season. Highest food conversion efficiency occurred during the first half of the year and declined during the second half of 1990. These results agree with whose earlier reported by Yaragina (1989) that the highest growth rate of cod in the southern part of the Barents Sea in 1984–1987 was recorded in winter (from December to March) in the period of seasonal cooling of waters and most plentiful food supply, except cod at age 4, for which the growth rate increased during summer (from May to July) due to preying on post-spawning euphausiids. According to Figs. 2, 3, 4, 5, and 6, the relative rate of increase in terms of weight $((w2-w1)/w1)$ in percentage was 119% by December 31 for cod at age 2, 137%, 117%, 116%, and 89% for cod at age 3, 4, 5 and 6 years, respectively.

With regard to the differences between cod stocks in the energy requirements, the annual metabolism cost as a percent of the energy budget in the Northeast Arctic cod is relatively high, specially during the second half of 1990 indicating that the immature part of the Barents Sea cod needs to consume 21.9% and 23.4% (overall mean during summer and autumn) of the maximum consumption in order to maintain such a metabolic demands and establishing a balance between the rates of food turnover against the increased demands for food caused by increased metabolic rates. In contrast to the total metabolic rates reported by Jobling (1982), who used the relationship between metabolism and size, we included specific dynamic action and activity multiplier in the energy budget which significantly increased the total metabolism. The total energy available for growth in the North Sea, Faroe and the Balsfjord cod is higher than in the Northeast Arctic cod, in part because of the temperature in the water inhabited by each cod stock and in part because the consumption rate is higher in the North Sea, the Faroe and the Balsfjord cod stocks (Table 4).

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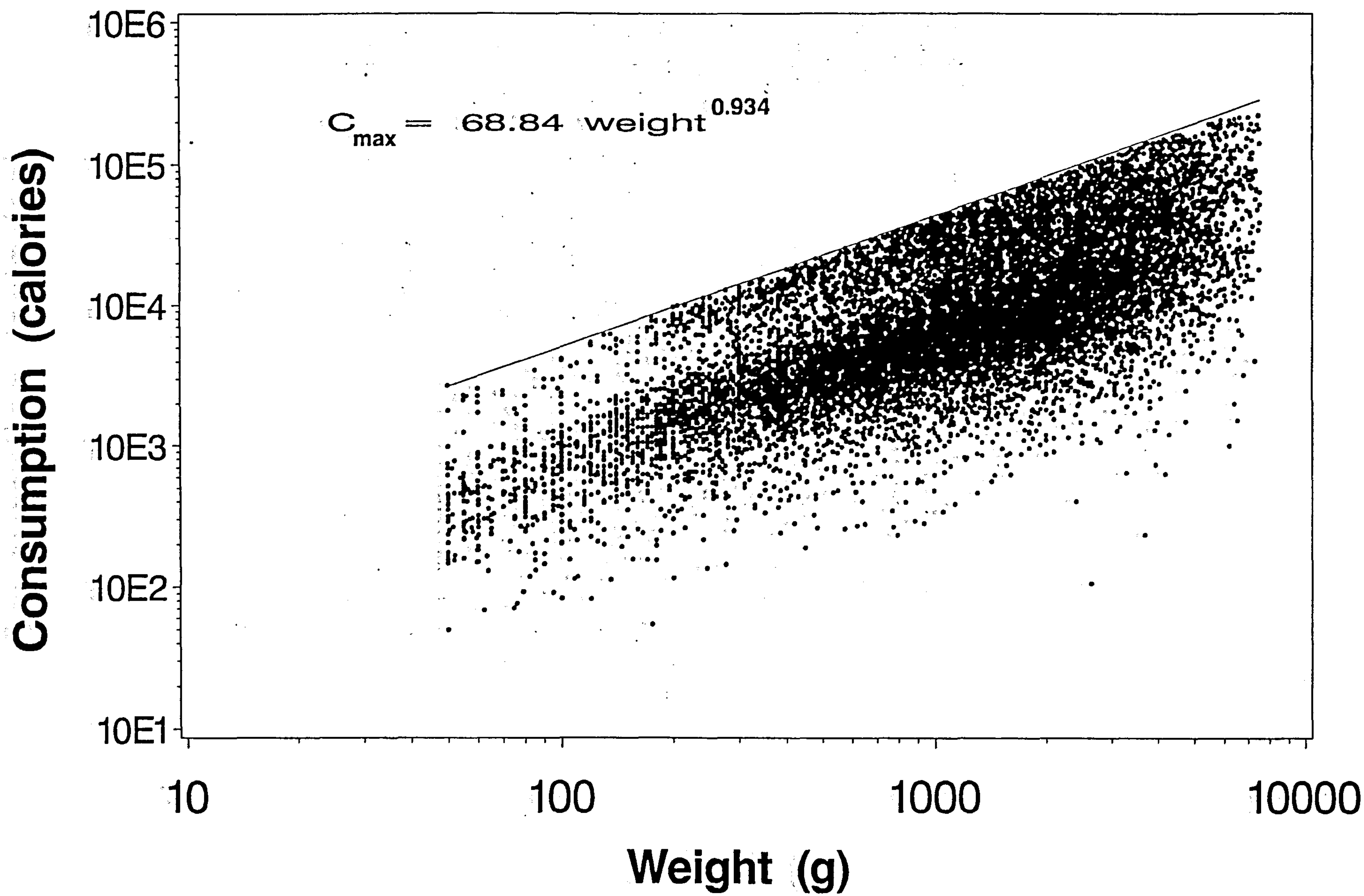
Fig. 1 Consumption(cal) to fish weight relationship with maximum consumption line during 1984–1991.



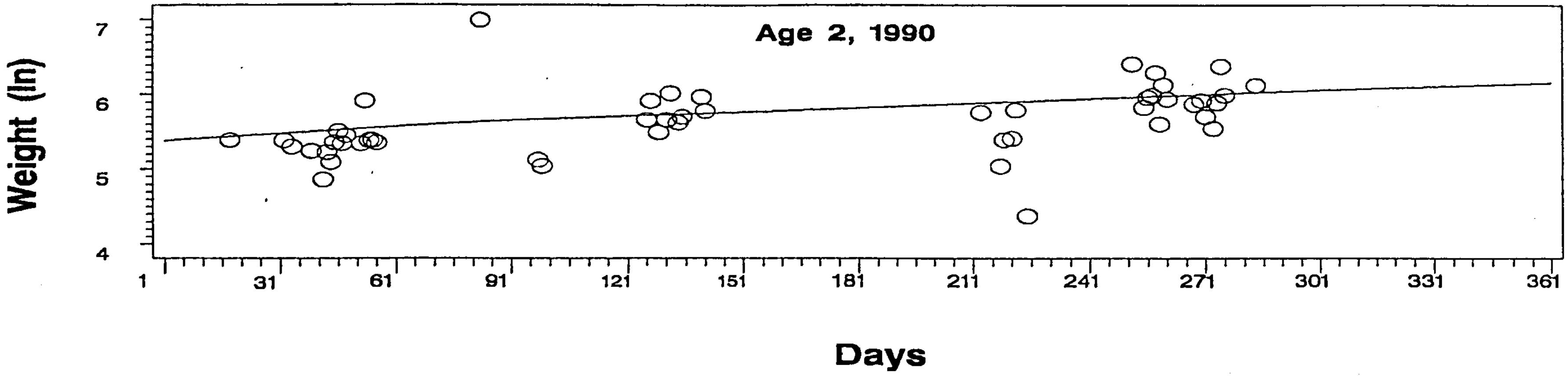


FIG.2. Fish mean weight(ln) by days (0 – observed, line – model output).

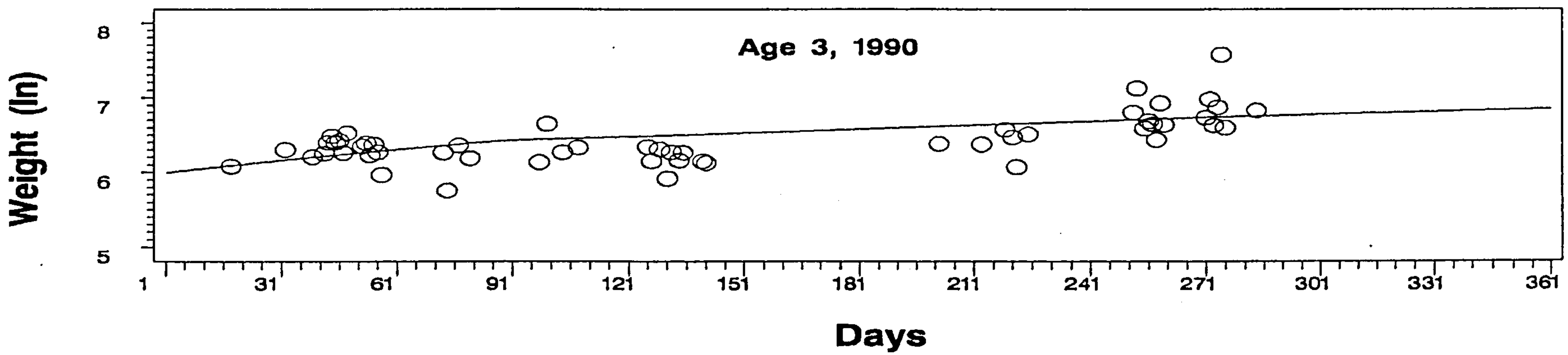


FIG.3. Fish mean weight(ln) by days(0 – observed, line – model output).

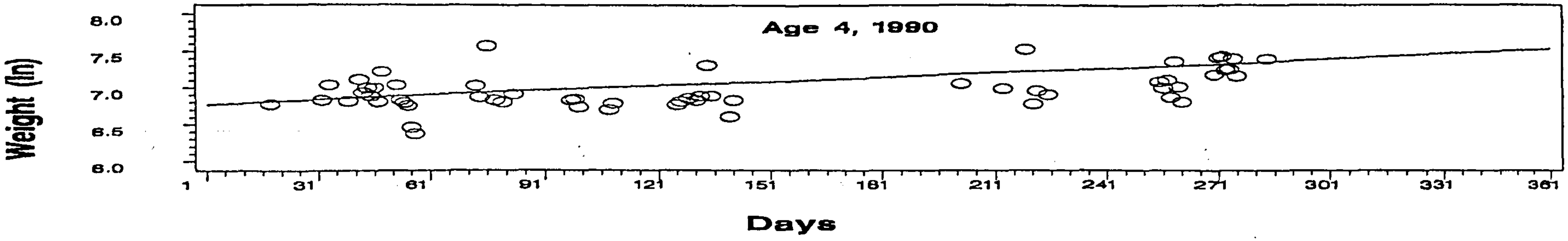


FIG.4. Fish mean weight(ln) by days(0 – observed, line – model output).

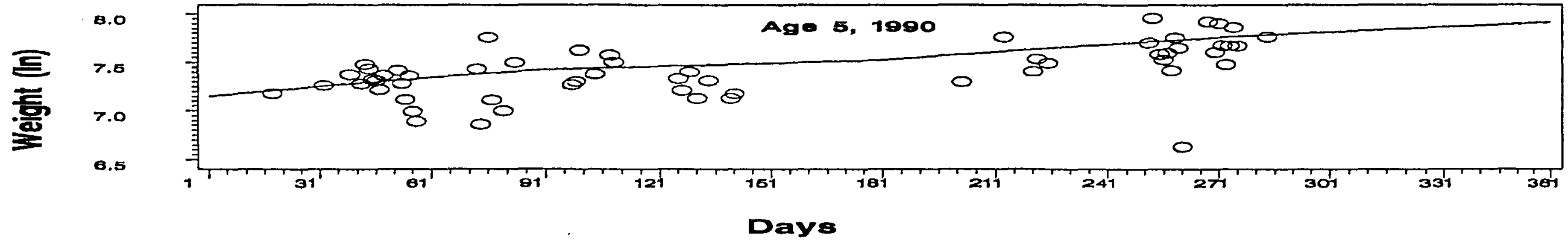


FIG.5. Fish mean weight(ln) by days(0 – observed, line – model output).

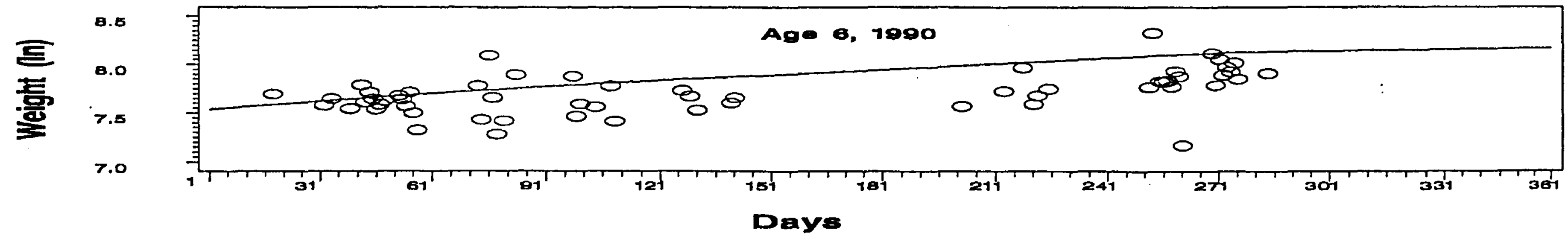


FIG.6. Fish mean weight(ln) by days(0 – observed, line – model output).