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The Propagation of cod *Gadus morhua* L.

GROWTH OF COD IN RELATION TO FISH SIZE AND RATION LEVEL

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ABSTRACT

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This study presents the main results of a series of growth experiments on cod with particular reference to ration size, size of the fish and growth and feeding in the spawning season. The experiments were started in 1977 in small laboratory tanks and continued in the period 1979-83 with small tanks, large outdoor tanks and net-pens.

The data indicate that cultured cod fed to satiation during their first two years of life grow two to five times faster than natural stocks in the North Atlantic.

The relation between growth rate and food intake was shown to be linear and the maintenance ration increased linearly with increasing size. Growth rate decreased with increasing size and a log-log transformation gave a good linear fit.

The fast growth of cod seemed to reduce age at first maturation and the cod stopped feeding for several weeks during the stage of late maturation and spawning. A larger weight loss was found for females than for males, average weight losses ranging from 16 to 27%.

INTRODUCTION

The growth of cod, *Gadus morhua* L. populations has in general been estimated from age and length data from commercial landings, tagging experiments and field research (Graham, 1934; Kohler, 1964; Daan, 1974). These data give a fair description of growth during the exploited phase of life, but little information on the juvenile stages.

Laboratory experiments have further examined the growth process in detail and in particular the fundamental relation between growth and food (Kohler, 1964; Edwards et al., 1972; Jones and Hislop, 1978), which in turn has been used in growth models (Daan, 1975; Jones and Johnston, 1977) or estimates of food-growth relations in wild populations (Jobling, 1982).

The food-growth relationship of cod has been shown to be linear up to the limit of appetite (Jones and Hislop, 1978; Jobling 1982), in contradiction to more complicated curvilinear forms (Brett, 1979; Ricker, 1979). If the linear form can be accepted, maintenance ration and net conversion efficiency are easily calculated. The present paper discusses these possibilities.

It is generally accepted that growth decreases with increasing size and Brett and Shelbourne (1975) found that a log-log transformation provided a good linear fit between growth rate and weight for salmonids. A similar study was made on cod in the present paper.

When a fish reaches maturity, the energy that might have been used for growth will be required for developing gonads and for making spawning migrations (Jones, 1976). A certain weight loss can be expected due to spawning and Daan (1975) assumed that the energy expenditure of reproduction was the same in both sexes.

There have been contradictory opinions as to whether or not cod feed at spawning time (Dambergs, 1964; Klemetsen, 1982; Rae, 1967; Waterman, 1968). The study followed separate groups of males and females through the spawning period to determine the extent of spawning and feeding in this period.

Cod is expected to be a future species for aquaculture. The main purpose of these studies was to examine the growth of cod in captivity with particular emphasis on how the two biotic factors of ration and size were related to growth. Early maturation and spawning is known to have a serious effect on salmonid farming. These factors were also examined in the present study.

MATERIALS AND METHODS

Experiments were conducted in the period July 1977 to January 1978 at the Institute of Marine Research, Bergen and April 1979 to June 1983 at Austevoll Marine Aquaculture Station.

Experiments in 1977 and 1978

Young cod were caught by drag-net and acclimated for two months in a concrete basin (36 m^3) before being transferred to the experimental tanks.

Ten dark green oval self-cleaning fiberglass tanks (175 l), modified after Brett et.al. (1971), were used in the experiments. Six of the tanks were equipped with recirculating pumps to create an adjustable water-current. The modifications on tank design, water flow and temperature regulation are described by Braaten (1976).

Temperature in the tanks was kept at near 8^{o}C, salinity at 34.8 $\pm$ 2 o/oo and oxygen between 90 and 100% saturation. Water flow ranged between 3-4 l/min and in tanks 1 to 6, a water current that ranged between 0.3 and 0.4 fish lengths per second was established. (Table 1)

A fluorescent light illuminated tanks 1 to 6 and was controlled by a time switch to give a 16-h day (0400-2000). Brightness was regulated for ½ hour when the light was switched on and off to create a gradual change from darkness to full light. Fish were fed by hand twice a day for five days a week and once on the sixth day.

Experiments from 1979 to 1983

Cod of various sizes were caught in traps and nets. After grading, the fish were acclimated for at least a month before the experiments started. Some experiments were also carried out with cod hatched and raised at the station, but no difference in survival or behaviour could be found between cultured and wild fish.

Small cod (50-200 g) were kept in oval growth tanks (Table 2) as in 1977, larger cod in outdoor circular fibre glass tanks and net-pens. The experiments in 1979 were performed in 3 m^3 (1 m deep) open tanks, later studies in 1.7 m^3 (1 m deep) covered tanks (Table 3). The tanks were dark green self cleaning with double pipes in the center. Water was put in at the surface through a perforated horizontal pipe which created a stable circular water flow.

The net-pens were part of a 20 room raft where each room (4x4x3 m) was made of a knotless seine of a 15 mm mesh size.

The tanks were cleaned every month at the time of measurements and nets were changed at regular intervals, depending on the extent of fouling. All experimental units with large fish (above 200 g) were fed three times per week, small fish 4-5 times per week.

Experimental tanks were supplied with water from 50 m depth which kept the temperature between 6 and 9^{o}C for eight months of the year (Fig. 1). The water temperature was not regulated but was relatively stable for long periods of time. Minor variations of ± 0.2^{o}C through a day was registered. Salinity varied slightly between 31 and 33 o/oo and oxygen was near 100% saturation.

The experimental conditions in the net pens were identical to those in the surface layer between zero and three meters. Temperature varied between 4 and 14^{o}C (Fig. 2).

Extreme low (2^{o}C) values in February/March and high (18^{o}C) values in July/August occurred for short periods (3-15 days). Average salinities ranged from 25 to 31 o/oo. All outdoor experimental units were exposed to artificial light at night throughout the year from spotlights surveying the area.

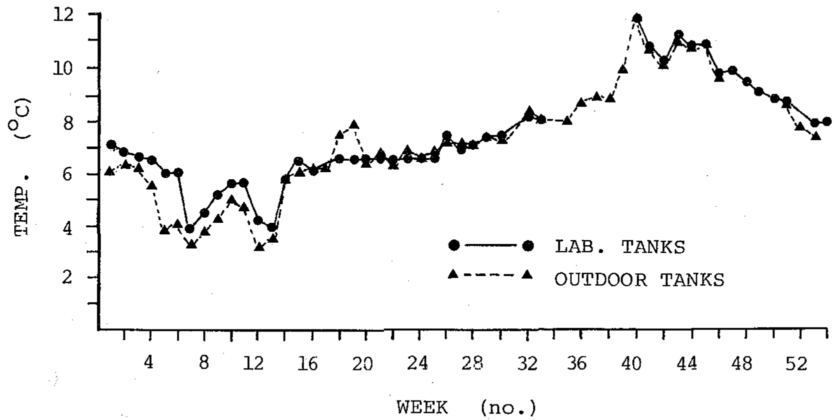

Fig. 1. Average weekly temperatures in laboratory tanks and outdoor tanks in 1980 at Austevoll marine aquaculture station.

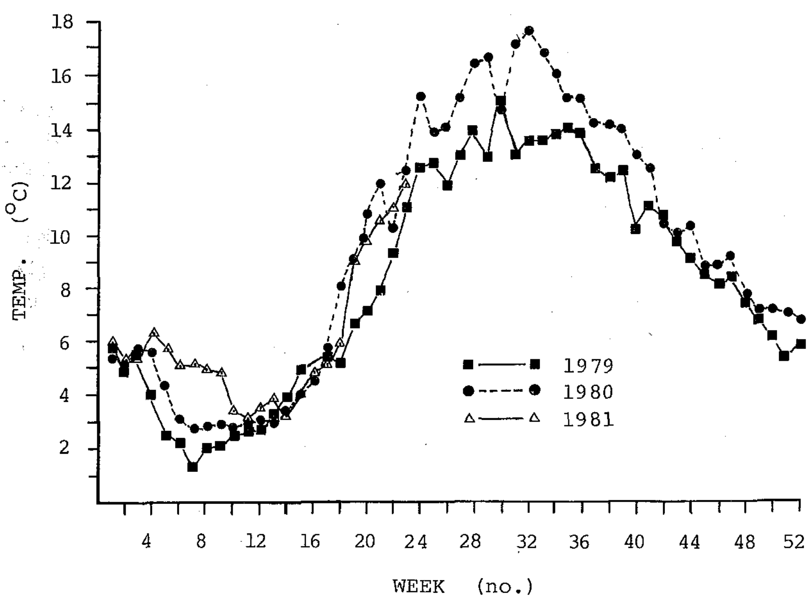

Fig. 2. Average weekly temperatures at 2 m depth at Austevoll marine aquaculture station.

Relation between food intake and growth

All fish were fed by hand either to a predescribed ration as percent of body weight per day, or to satiation. Satiation in these experiments was considered to have been reached when appetite declined substantially. Loss of food was negligible in tank experiments since they soon learned to pick up food from the bottom. The period between weighing was extended from two weeks in the 1977-78 series (Table 1) to four or five weeks in later experiments (Table 2-5), to reduce unfavourable effects of stress from handling. Within each tank, ration levels were either kept constant or alternated between growth periods. Table 1-5 give the vital experimental conditions for the various experiments. Groups of top graded cultured cod of the 1981 and 1982 were raised in net-pens and compared to wild fish raised in tanks and net-pens.

Growth and feeding during spawning

All fish were classified according to sex and stage of maturation in the spawning season. Running males were easily detected while prespawning females were often labelled uncertain.

In January 1983 a sample of 49 cod (1.5-2.0 kg) was separated into three groups (running males, running females and uncertain females) and followed throughout the spawning period. Each fish was marked with a FD-67c Floyd anchor tag and examined at 3-4 week intervals. When an uncertain female became running or the fish were classified as post spawners, they were transferred to a new tank.

The cod were fed regularly every second day and surplus feed removed a few hours later. Gonadal products were not collected.

Collection and handling of growth data

Fish were fasted at least two days prior to weighing. After anaesthetisation in a solution of benzocaine in sea water

TABLE 1

Initial and terminal size of cod in experiments in small laboratory tanks 1977/78, and vital experimental conditions. Standard deviation is shown in parenthesis.

Tank no.	1	2	3	4	5	6	8	9	10	11
Mean temp. (°C)	8.3- (0.6)	8.3- (0.6)	8.2- (0.6)	8.2- (0.6)	8.2- (0.6)	8.3- (0.6)	8.6- (0.5)	8.4- (0.5)	8.5- (0.5)	8.4 (0.5)
Total test days	125	125	160	160	160	55	214	126	149	126
Interval between weighing (d)	14	13-14	13-18	13-18	13-18	13-14	12-24	18-15	12-15	12-15
Initial no. of fish per tank	14	12	14	12	7	4	12	1	3	1
Initial length (cm)	17.4 (0.9)	20.9 (0.6)	22.5 (0.9)	25.0 (0.8)	29.1 (1.0)	32.7 (0.6)	15.0 (0.5)	34.6	19.4	26.5
Initial weight (g)	44.4 (6.2)	82.7 (9.5)	110.0 (12.1)	150.6 (11.0)	252.5 (29.1)	370.9 (19.7)	28.2 (3.9)	517.7	60.9 (2.6)	171.9
Terminal length (cm)	21.0 (1.4)	23.9 (0.6)	28.7 (1.5)	33.2 (0.8)	35.8 (0.4)	-	20.8 (1.9)	38.8	25.9 (2.6)	33.6
Terminal weight (g)	84.6 (18.8)	137.0 (9.3)	256.1 (42.7)	358.1 (34.3)	481.5 (63.1)	471.3 (60.2)	82.3 (23.7)	719.2	179.2 (60.4)	397.7
Range of ration-levels (% wet wt/d)	0.8- 4.5	0.8- 3.2	0.8- 3.1	0.8 3.0	0.8- 2.9	0.8- 3.1	0.9- 3.7	0.9- 2.2	1.0- 4.2	2.0- 2.9
Water velocity (cm/sec)	5.9	7.2	8.1	8.0	9.5	11.6	6.4			

TABLE 2

Initial and terminal size of cod in experiments in small laboratory tanks 1980/81, and vital experimental conditions. Standard deviation is shown in parenthesis.

Tank no.	10	15**	16**	14**	18	11	12	13	14	19
Range of temp. (°C)	6.3-8.9	6.3-8.9	6.3-7.8	6.3-7.8	6.3-8.9	6.3-8.9	6.3-8.9	6.3-8.9	6.3-8.9	6.3-8.9
Total test days	70	68	33	33	68	68	68	68	68	70
Interval between weighing (d)	35	33-35	33	33	33-35	33-35	33-55	3-35	3-35	35
Initial no. of fish per tank	5	9	5	4	2	4	4	5	5	4
Initial length (cm)	17.6 (1.4)	24.7 (1.9*)	23.6 (0.9)	21.5 (1.6)	20.7 (2.8*)	19.0 (1.8*)	18.5 (3.0*)	19.9 (2.2*)	18.8 (2.1*)	39.5
Initial weight (g)	55.2 (13.3)	152.4 (36.9*)	114.7 (11.6)	93.6 (19.3)	90.9 (34.2*)	68.1 (20.8*)	71.2 (39.9*)	80.4 (26.7*)	80.0 (27.5*)	799.0
Terminal length (cm)	18.3 (1.9)	27.6 (0.8)	23.7 (1.0)	21.8 (1.4)	23.8 (0.2)	20.0 (1.0)	19.7 (0.6)	24.9 (0.2)	26.9 (0.8)	41.1
Terminal weight (g)	51.6 (18.0)	189.9 (24.5)	155.5 (15.4)	86.3 (18.4)	112.2 (4.1)	75.7 (9.5)	75.2 (7.1)	163.3 (10.8)	227.1 (29.7)	804.1
Range of ration-levels (% wet wt/d)	0	0.25	0.26	0.27	0.4-0.6	0.9	1.6	2.0-2.1	1.5-2.3	0.25

** Wild fish

* The fish were restocked after the first growth period due to a large variation in size.

TABLE 3

Initial and terminal size of cod in experiments in outdoor 3 m^3 tanks (T-1, T-2, T-3) and 1.7 m^3 tanks (T-4, T-5, T-6) 1979/80, and vital experimental conditions. Standard deviation is shown in parenthesis.

Tank no.	T-1	T-2	T-3	T-4	T-5	T-6
Range of temp. (°C)	6.3-12.8	6.3-12.0	6.3-12.0	3.2-7.8	3.2-7.8	3.2-7.8
Total test days	267	267	267	147	147	147
Interval between weighing (d)	31-36	31-36	31-36	30-47	29-47	29-47
Initial no. of fish per tank	14-46**	36-59**	21-45**	29	30	21
Initial length (cm)	31.3 (2.2)	36.5 (2.3)	39.9 (1.2)	36.2 (1.7)	42.6 (1.9)	48.7 (1.9)
Initial weight (g)	306.4 (56.7)	496.0 (56.5)	683.2 (58.5)	498.8 (44.4)	821.9 (68.7)	1324.7 (71.5)
Terminal length (cm)	43.9 (2.5)	43.8 (2.2)	46.8 (1.9)	2.9 (2.6)	46.4 (27.1)	52.5 (2.3)
Terminal weight (g)	1066.6 (156.0)	972.0 (137.8)	1123.6 (161.9)	978.8 (195.7)	114.6 (216.0)	1836.6 (266.3)
Range of ration-levels (% wet wt/d)	0.9-2.3	0.5-1.6	0.3-1.5	1.2-1.7	0.7-0.9	0.6-1.1

** The groups were graded and restocked after each weighing in the period 26.4-1.8-79.

TABLE 4

Initial and terminal size of cod in experiments in 17 m^3 outdoor tanks 1980/81, and vital experimental conditions. Stnandard deviation is shown in parenthesis.

Tank no.	T-21	T-22	T-23	T-24	T-25	T-26
Range of temp. (°C)	4.3-8.8	4.3-8.8	4.3-8.8	4.3-8.8	4.3-8.8	4.3-8.8
Total test days	168	168	168	168	168	168
Interval between weighing (d)	26-37	26-37	26-37	26-37	26-37	26-37
Initial no. of fish per tank	13	12	12	12	12	10
Initial length (cm)	30.6 (2.5)	36.2 (1.9)	31.0 (2.3)	37.1 (2.1)	30.4 (2.3)	37.3 (1.6)
Initial weight (g)	293.9 (68.9)	494.2 (75.3)	312.9 (52.6)	519.4 (67.4)	274.4 (55.0)	494.8 (77.9)
Terminal length (cm)	37.3 (1.2)	42.8 (1.9)	37.8 (2.5)	40.4 (2.6)	31.7 (2.4)	36.7 (1.4)
Terminal weight (g)	626.0 (80.6)	955.9 (180.6)	617.6 (144.6)	678.6 (219.7)	283.4 (71.8)	306.6 (60.4)
Range of ration-levels (% wet wt/d)	0.6-2.4	0.6-2.0	0.6-1.3	0.6-0.7	0.3-0.4	0

TABLE 5

Initial and terminal size of cod in experiments in 50 m^3 net-pens 1979 (1, 2), 1980 (3), 1980/82 (4, 5), and vital experimental conditions. Standard deviation is shown in parenthesis.

Net-pen no.	1	2	3	4	5
Range of temp. (°C)	2.0-6.0	2.0-6.0	2.7-15.1	2.1-17.6	2.1-17.6
Total test days	57	58	146	533	533
Interval between weighing (d)	57	58	29-48	32-91	32-91
Initial no. of fish per pen	24	41	51	31	41
Initial length (cm)	25.3 (3.2)	31.8 (2.8)	45.4 (2.0)	39.7 (3.8)	55.0 (5.5)
Initial weight (g)	145.5 (37.3)	308.5 (57.8)	1063.7 (77.5)	684.5 (228.3)	1913.3 (769.1)
Terminal length (cm)	27.6 (2.0)	33.6 (1.8)	50.3 (2.9)	58.4 (5.4)	66.3 (7.4)
Terminal weight (g)	217.5 (56.9)	415.5 (82.6)	1558.7 (328.2)	3239.4 (1079.9)	4302.1 (1295.3)
Range of ration-levels (% wet wt/d)	1.0	1.2	0.8-1.1	0.01-1.5	0.01-1.0

(Egidius, 1973) the small fish (<100 g) were measured with a digital electronic balance to the nearest 0.1 g, and to 1 g for the remainder. Total length was measured to the nearest mm for small fish (less than 50 cm), and to the nearest 0.5 cm for larger fish.

All growth data are based on average wet weight values from groups of experimental fish. Weights have been adjusted where mortalities occurred. Instantaneous growth rates were calculated from the equation

$G = (\ln W_{t_1} - \ln W_{t_0})/(T_1-T_0) \times 100$, where

G = instantaneous growth rate as a percentage of body weight per day, W_{t_1} = final weight (g), W_t = initial weight (g), T_1 = final time (d) and T_0 = starting time (d).

Growth increments were expressed as gram per fish per day. Food intake was calculated in per cent of wet body weight and in gram per fish per day. In this study, growth increment and food intake were converted to kcal by using the gross energies (9.45 kcal/g of fat, 5.65 kcal/g of protein and 4.0 kcal/g of starch), (Brody, 1945).

Diet composition and proximate analysis

The composition of the experimental diet used in 1977/78 is given in Table 6. Saithe fillet, which was used as the protein source, contained 0.5% fat, 17.0% protein (Nx6.25) and 20.0% dry matter. Capelin oil and dextrinized potato starch were used as energy supplies. The feed was processed into moist pellets (5 mm in diameter), frozen and given to the fish half-thawed.

Freshly thawed capelin were given as food in all later experiments. Only lean capelin caught in the spawning season were used and small variations in caloric content existed.

The energy value of 1.67 ± 0.08 kcal/g wet weight used in the caloric calculations represents an average value of five samples.

TABLE 6

Composition of the experimental diet in experiments at the institute of marine research, 1977/78.

Ingredients	g/kg wet weight
Saithe (*Pollachius virens*) fillet	895
Capelin (*Mallotus villosus*) oil	56
Dextrin from potato starch	77
Carboxymethylcellulose	8
Vitamin mixture[1]	12
Mineral mixture[2]	3
Kcal/g wet weight (gross energies)	1.71
Total energy from protein (%)	48.0

1,2, Lied and Rosenlund, 1984.

Crude nutrient analysis of capelin showed a variation in dry matter of 262.4 $\pm$ 7.6 g/kg, in raw protein of 139.8 $\pm$ 3.6 g/kg wet weight, in raw fat of 94.2 $\pm$ 6.1 g/kg wet weight and in ash of 23 $\pm$ 3.6 g/kg wet weight.

In some experiments, samples of cod (3-5) were analysed. The fish were killed by a blow on the head, wrapped in tinfoil and frozen immediately.

A caloric value of 1.71 $\pm$ 0.18 kcal/g wet weight was calculated as the average value of 19 samples representing 13 experiments with cod from 9,3 to 1691 g.

Each analysis of either protein or fat represents a pooled value of three samples.

Aliquots were digested for the determination of nitrogen by the micro-Kjeldahl technique in a thermostatically-regulated heating block (TECATOR 40). Nitrogen was determined in the digest as described by Crooke and Simpson (1971) and protein as Nx6.25.

Fat was analysed by gravimetric methods after extraction by diethyl ether in a Soxlet extractor. Water content was determined by freeze-drying samples *in vacuo* for 17 h, or by heating for 4 h at 105 °C, and ash content by igniting for 4 h at 550°C in a small muffle furnace.

Since most experiments lasted several months with large temperature variations, the results were separated into temperature groups. The long duration of each experiment resulted in a large size distribution of cod. It was therefore decided to treat the growth data in size groups rather than separate experiments.

RESULTS

Growth curve for cod

The growth in weight of cod in captivity fed ad libitum followed a typical sigmoid pattern, interrupted by loss of weight during spawning, but thereafter increasing almost linearly to the next spawning period (Fig. 3). The curves were fitted by eye and the data are derived from several experiments in the period 1979-1983.

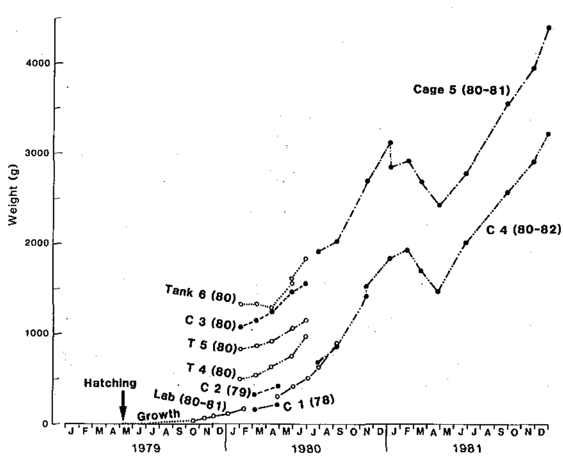

Fig. 3. Growth of cod from hatching to beyond maturation. The curves represent various experiments in laboratory tanks, outdoor tanks and net-pens (cages) in the period 1978-82.

All growth data were calculated from day zero at hatching (Øiestad and Kvenseth, 1981) and results from various years have been adjusted to represent development and growth in one growth period. The wild fish is probably one year older than the cultured fish of the same size due to a faster growth during the first year.

By using the logarithms of weight against age in days, growth stanzas are indicated (Fig. 4). Growth was exponential within each stanza (R = 0.99) and could be described by the equation $W = a \cdot \exp b \cdot t$ where W is weight in grams, t time in days and a and b constants. It is uncertain if the development of growth stanzas are entirely artificial or a result of growth variations due to size and environmental conditions.

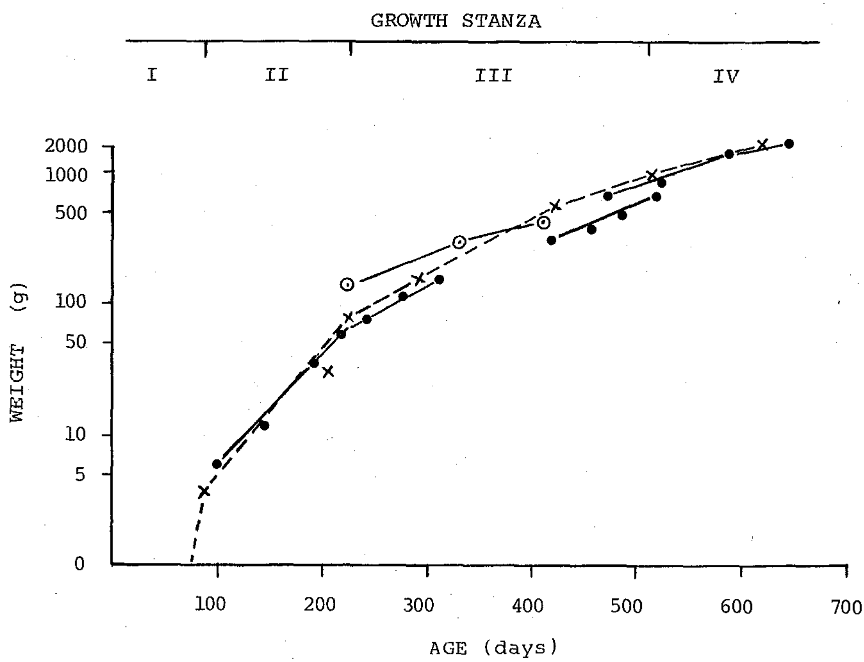

Fig. 4. Prespawning growth of cod in relation to age and development of growth stanzas.

.______. wild cod in culture
x-----x cultured cod, 1981 generation
O______O cultured cod, 1982 generation.

The growth of top graded cultured cod of the 1981 and 1982 generation was almost identical to that of wild cultured cod as seen in Fig. 4. This strongly indicates that cod of similar size grow at the same rate in culture conditions, independant of age or origin. Origin in this connection refers to hatched in culture or wild cod which both have been grown in culture.

The larval stages, metamorphosis and the first three months can be subdivided into several distinct growth periods, but in this paper these are called the initial period (I). The second period seemed to extend from 3-6 to 90 g (II) with growth rates between 2 and 1.4%/day. The third growth period ranged from 90 to 8-900 g with growth rates between 1.7 and 0.8%/day, and the fourth period between 1000 and 2000 g with growth rates from 0.7 to 0.2%/day for immature fish. Larger fish exhibited maximum growth rates of 0.2-0.3%/day.

The same group of fish was followed until they spawned 21 months after hatching. Their growth rate declined with the onset of maturation.

Growth and feeding in the spawning period

Growth rate decreased gradually as the cod approached spawning (Fig. 5) and was negative for about three months. Both running males and females stopped feeding completely in the early spawning period (Table 7) and the small amounts given as indicated by Table 7 were totally ignored. Active feeding was resumed in April apparently among running cod of both sexes. It was impossible to determine either the exact time of the onset or the completion of spawning for each individual fish. The data in Table 7 and Fig. 5 therefore only indicate the time and extent of feeding and growth.

Both males and females followed the growth pattern found for cod in 1981 (Fig. 5). All males were running when the experiment started and sperm were found until the middle of May. Only 26% of the females were ready to spawn in January and 25% females had still small amounts of eggs left when the experiments terminated in June.

TABLE 7

Growth and feeding of cod in the spawning season. Various categories of males and females (1.4-1.9 kg) were kept in separate tanks at average weekly temperatures from 5.8 to 8°C. All fish were redistributed after each growth period according to their sexual development. Growth rate (G) and ration (R) are expressed as % wet wt/day.

	MALES						FEMALES								
	Running			Spent			Maturing			Running			Spent		
Period	G%	R%	n	G%	R%	n	G%	R%	n	G%	R%	n	G%	R%	n
25.1-24.2	-0.25	0.002	24	-	-	-	0.1	0.37	20	-0.5	0.02	5	-	-	-
24.2-21.3	-0.19	0	19	-	-	-	-0.15	0.06	7	-0.56	0.09	4	-	-	-
										-0.53	0.04	13			
21.3-06.4	-0.01	0.1	19	-	-	-	-0.14	0.20	4	-0.38	0.52	16	0.65	1.06	2
06.4-28.4	-0.02	0.29	19	-	-	-	0.22	0.63	2	-0.23	0.74	16	0.29	1.13	4
28.4-19.5	0.27	0.85	19	-	-	-	-	-	-	0.31	1.07	15	0.10	0.84	5
19.5-09.6	-	-	-	0.21	1.06	19	-	-	-	0.39	1.18	5	0.61	1.36	15

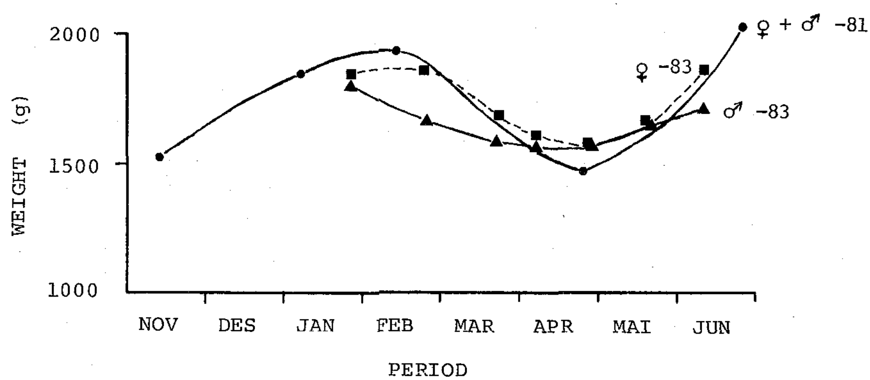

Fig. 5. Weight changes in the spawning season in cod *Gadus morhua* reared in a 50 m^3 net-pen (1981), and in separate indoor 1.7 m^3 tanks for males and females (1983).

The amount of gonadal products produced were calculated as the total weight loss in the period for each individual cod. Active feeding and positive growth was interpreted as post-spawning conditions. A Student t-test with unequal variances showed a significantly larger weight loss ($p<0.001$) among females (27.4%) than males (15.9%) on the assumption that all spawning took place in the experimental period and without feeding (Table 8 a). There was a significant correlation between fish size at the onset of spawning and weight loss due to spawning, $p<0.001$ for females and $p<0.05$ for males, but large variations occurred in both sexes (Table 8 a). Since all the males were running when the experiment started some inaccuracy was expected.

TABLE 8

Fish weight and weight loss in the spawning period. Average values from individual tagged cod. Total weight loss in the spawning season (a). Weight loss in the period January 26 - May 19 for wild fish in culture (b) and cultured cod of the 1981 generation (c).

	Sex	N_1	Range	Average	S.D.	%	S.D.	n_2
a)	Male	19	1114 - 3051	1797	493	-15.9	4.7	19
	Female	26	1024 - 2898	1789	406	-26.9	9.7	20
b)	Male	19	1114 - 3051	1797	43	-10.0	7.4	19
	Female	21	1024 - 2898	1771	520	-14.8	13.8	21
c)	Male	18	1195 - 2640	1733	371	+ 2.3	10.8	18
	Female	30	1106 - 2380	1667	357	- 0.8	19.5	30

Cultured cod of the 1981 generation raised in net-pens were measured quarterly and compared with the selected groups of males and females. The group (n-48) consisted in January 1983 of 18 running males, 6 mature females and the remaining 24 cod were classified as possible maturing females. They were examined again in May, and 4 males and one female were still running, while 43 were post-spawning individuals. Table 8 c shows the average weight loss or gain in the period for males and females of the cultured 1981 generation. The data can only indicate the extent of spawning since some individuals had started active feeding. To compare these results with the experimental data on males and females already described, it was necessary to use the results obtained in the same time period. The data showed a significant difference in weight loss between the two groups ($p<0.001$) for males and ($p<0.001$) for females. No significant difference in weight loss was found between males and females of the cultured cod.

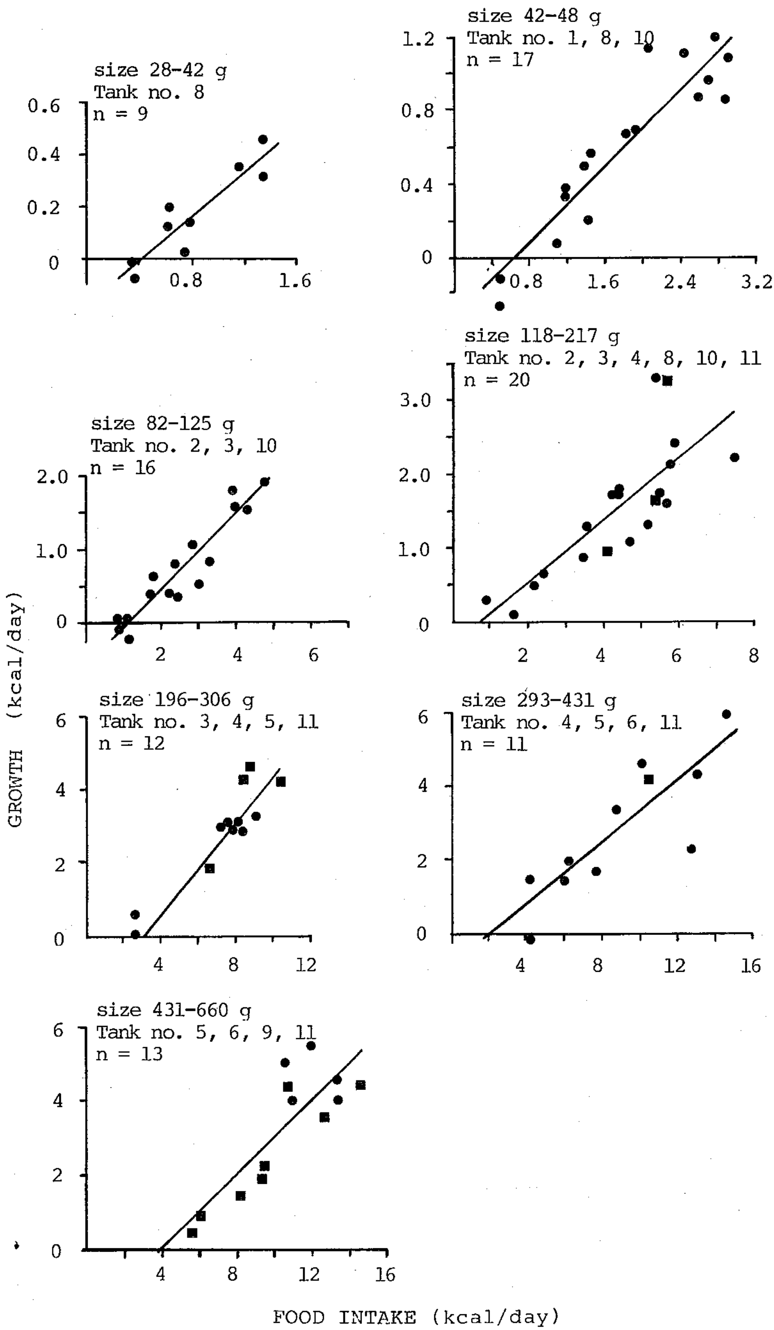

Fig. 6. Growth in relation to food intake (kcal/fish/day) for cod *Gadus morhua* of various sizes at 8.5 ± 0.5°C in 1977/78.

● Groups of fish
■ Single fish

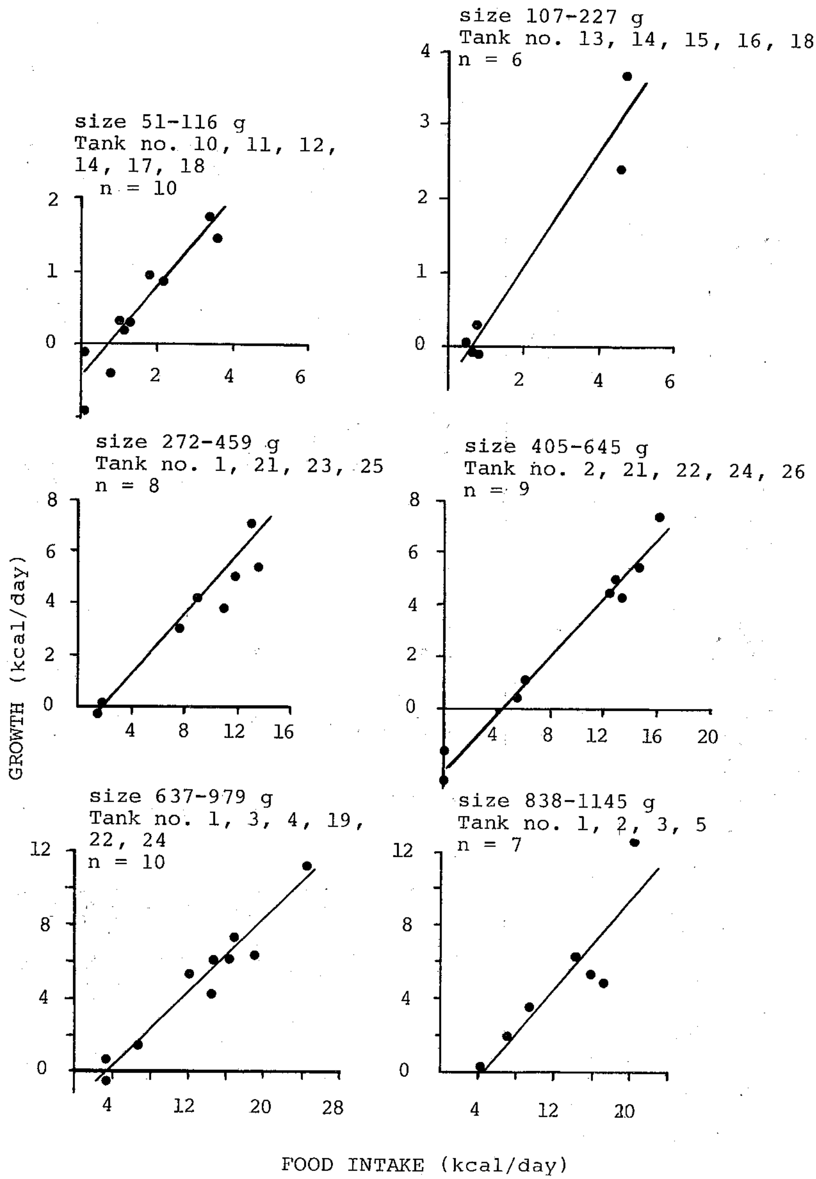

Fig. 7. Growth in relation to food intake (kcal/fish/day) for cod *Gadus morhua* of various sizes at 6-9°C in 1979/81. Each point represents mean values per tank.

TABLE 9

Summary of growth-ration data for cod *Gadus morhua* of different sizes at 6 - 9°C. Values of a and b represent the intercept and slope in the equation: Growth G (kcal/fish/day = a + bF (kcal/fish/day).

Moist pell. exp. 1978/79, Capelin exp. 1979/81.
** p<0.01 *** p<0.001

Temperature °C	No.of. exp.	Fish weight (g) Range	Mean	n	Food type	Parameters in equation a	b	R_{maint}	R_2	Signif.
8.6 ± 0.5	9	28- 42	35	12	Moist p.	-0.17	0.42	0.40	0.83	* * *
8.5 ± 0.5	17	42- 84	63	27	" "	-0.33	0.52	0.63	0.83	* * *
8.3 ± 0.6	16	82- 125	106	28	" "	-0.60	0.52	1.15	0.90	* * *
8.3 ± 0.6	20	118- 217	160	38	" "	0.42	0.44	0.95	0.63	* * *
8.4 ± 0.5	12	196- 306	252	34	" "	-1.16	0.52	2.15	0.87	* * *
8.3 ± 0.6	11	293- 431	381	16	" "	-0.94	0.43	2.19	0.70	* *
8.4 ± 0.5	13	431- 660	473	9	" "	-1.94	0.50	3.88	0.69	* * *
6.3 - 8.9	10	51- 116	82	41	Capelin	-0.44	0.61	0.72	0.90	* * *
" "	6	107- 227	152	28	"	-0.48	0.75	0.64	0.94	* *
5.4 - 9.1	8	272- 459	351	146	"	-0.83	0.51	1.63	0.92	* * *
" "	9	405- 645	536	219	"	-2.29	0.55	4.16	0.98	* * *
6.0 - 9.4	10	637- 979	760	188	"	-1.70	0.50	3.40	0.95	* * *
" "	7	838-1145	1004	201	"	-2.69	0.60	4.48	0.78	* *

RELATION BETWEEN FOOD INTAKE AND GROWTH

The relation between food intake (F) and (G) growth seemed to be approximately linear as seen in Fig. 6 and 7 and regression lines of the form G = a + b F are presented in Table 9. Both G and F are expressed in kcal/fish/day and separate graphs were plotted for fish with different body weights to allow for the effect of fish size and growth.

Since the conditions were different in the two series (1977-78 and 1979-81) separate graphs were constructed.

All the regression coefficients (slopes) were significant ($p<0.01$) and Table 9 indicates a difference between the two series. Since each point represents the average value of a number of cod, some variation was expected.

As presented earlier by Jones and Hislop (1978) and Jobling (1982) it is of interest to define the food level at zero growth F = -a/b which gives the maintenance ration (R_m). The equation may also be written

$$b = G/(F - Rm)$$

where the slope b gives an estimate of the net efficiencies of conversion of food into growth.

Table 9 shows that Rm increases with increasing fish size and the data can be fitted to a straight line by logarithmic transformation of the form

$$\ln Rm = \ln a' + b' \ln W \text{ or } Rm = a'.W^{b'}$$

where the slope b' indicates the increase in metabolism with size and a' is dependent on several factors such as temperature and nutritional status. Table 10 presents the regressions for the two experimental series and for the whole period. All regression coefficients were significant ($p<0.01$).

TABLE 10.

Statistics for the regressions of maintenance ration against body weight of cod.

** p<0.01 *** p<0.001

		Regression coefficients			
Exp.series	n	a'	b'	R^2	Level of signific.
1977-78	7	0.0226	0.803	0.94	* * *
1979-81	6	0.0127	0.856	0.89	* *
1977-81	13	0.0245	0.765	0.89	* * *

The data in Table 10 gave no evidence of variation in net efficiency with size.

The food-growth data were also calculated in per cent of body weight per day. A similar set of linear equations were established which all were significant ($p<0.01$).

Growth data from all experiments in tanks and cages representing cod fed ad libitum rations at temperatures between 6 and 9°C, were examined in relation to fish size. A log-log transformation provided a good linear relation (Fig. 8) between growth rate and weight of cod where

$$G = 9.68 \cdot W^{-0.45} \qquad R^2 = 0.73 \ (p < 0.01)$$

where G represents growth rate (% Wt/day) and W the weight of cod (g).

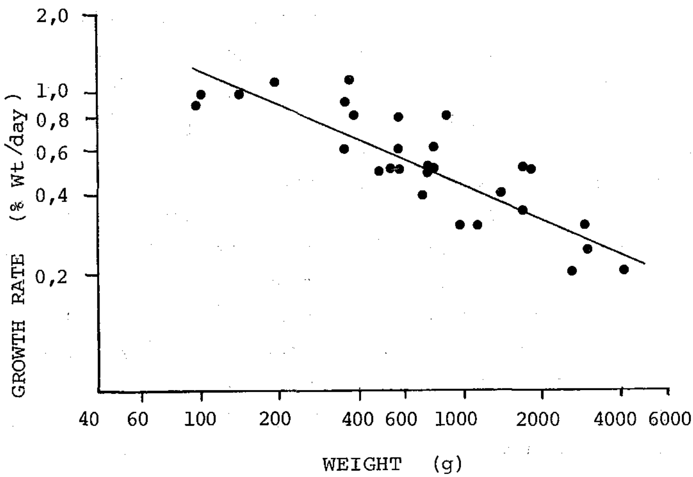

Fig. 8. The growth rate - weight relation for cod *Gadus morhua* at 8.5 °C fed to satiation.

DISCUSSION

The present study shows that cod in culture conditions fed to satiation at regular intervals exhibit a growth rate that far exceeds natural stocks. The growth curves were mainly based on experiments on wild fish of unknown age and supplemented with data from larvae reared in an inlet (Øiestad and Kvenseth, 1981). The lower curve in Fig. 3 represents growth from hatching to maturation, spawning and post-spawning while the upper curve indicates further growth through a second spawning. Later growth experiments with top graded cultured juveniles of the 1981 and 1982 generation confirmed the shape of the curve and showed that growth could be further improved from 275 g one year after hatching to 320 g. These results are in agreement with experiments in Lowestoft (Howell and Bromley, 1983) where 6 month hatchery reared cod (12 cm) were fed at ambient temperatures (6-12°C) and grew to a size of 500 g in 42 weeks, which corresponds to 270 g after 12 months.

A comparison in size between natural and cultured cod (Table 11) indicates that cultured cod have a growth rate during their first two years of life that is two to five times faster than Faroe and North Sea cod stocks (Jones, 1978) or cod from Balsfjord in Northern Norway (Jobling, 1982). The North Sea cod is one of the fastest growing stocks in the North Atlantic (Jones and Johnston, 1977). Age group I from Balsfjord was evidently larger but hardly representative due to a small sample size (n=7) and the selective sampling method (M. Jobling, University of Tromsø, personal communication, 1983). Little information is available on the growth of juvenile cod younger than class II cod since these groups are not fully recruited to the fishery and poorly represented in the catches (Daan, 1974).

According to Jones and Johnston (1977) there is no such thing as "a cod growth rate". The present data represent the growth of cod in culture under conditions typical of the

TABLE 11

A comparison of fish weight (W) and gain (Wg) in grams of North Sea cod, Faroe cod (Jones, 1978), Balsfjord cod (Jobling 1982), wild cod in culture at Austevoll and cultured cod of the 1981 and 1982 generation, age class 1 is estimated to be 9 months old on January 1.

AGE	NORTH SEA		FAROE		BALSFJORD		AUSTEVOLL WILD/CULT.		CULTURE -81	-82	CULTU -8
CLASS	W	Wg	W	Wg	W	Wg	W	Wg	W	Wg	W
1	42				(138)		110'		140		22
		523				145		1690		1398	
2	565		657		283		1800''		1530		
		1121		769		375		1400			
3	1686		1426		658		3200''				
		1946		988		362		1150			
4	3632		2414		1020		4400''				

' - estimated age.
'' - unknown age of cultured wild cod from Austevoll

surface waters of Western Norway. However, they give an idea of the growth potential of cod and support Love (1980) in his conclusion that food availability and temperature act as limiting factors in growth.

The largest weight gain was attained during the first two years after which a decrease occurred due to maturation and spawning.

Oosthuizen and Daan (1974) found that North Sea cod matured during their second year of life and 50% maturation occurred at a weight of 1505 g for males and 2212 g for females. The present data support the evidence that males mature at a younger age and a smaller size than females (Powles, 1958; Thurow, 1970; Oosthuizen and Daan, 1974).

The high incidence of spawning in the 1981 generation of cultured cod strongly indicates that the fast growth was a major reason for early maturation. Several investigations on a variety of species has shown that the age of first maturation may be modified by factors influencing growth rate (Alm, 1959; Koto, 1975; Hallingstad, 1978; Tofteberg, 1982; Nævdal, 1983; Gall, 1983). There seems to be a minimum threshold body weight for sexual maturation of juveniles and fast growing individuals may have a lower threshold than those of average growth rate.

The total weight loss in the spawning period included spawning products, changes in water content and energy losses associated with late maturation and spawning. The calculated weight loss of 16 and 27% for males and females corresponds well with the gonadal weights for Baltic cod of 13 and 28% respectively of the weight of the fish (Chrzan, 1950). Spawning products can constitute up to 30% of the total body weight (Bagenal, 1967), and weight loss in some of the present female cod was as large as 45%. Since the weight losses were calculated as weight difference it was not possible to determine the amount spent compared to the other losses.

The seasonal variations in water content of cod muscle are reported to vary between 3% (Love, 1960) and 1% (Eliassen and Vahl, 1982) and are greatest during the spawning period.

The seasonal changes in water, fat and protein contents of muscle and liver have been related to gonadal growth and processes associated with spawning (Love, 1970; Shulman, 1974).

The experiments showed clearly that both males and females stopped feeding for several weeks before and during spawning. This agrees with the findings of Cushing (1966), Rae (1967) and Waterman (1968). The cod from Nova Scotia (Dahmbergs, 1964) and Balsfjord (Klemetsen, 1982) fed throughout the year and spawning seemed not to affect food intake.

There is still a lot of uncertainty about feeding and spawning, but the present results and observations elsewhere indicate that feeding during late maturation and spawning is related to size, geographical distribution, environmental conditions and possibly nutritional status.

The fundamental relationship between growth rate (G) and food intake (R) holds much of the key to understanding the action of environmental factors on growth (Brett, 1979). The G - R relation in the present experiments was found to be linear for all size groups at temperatures between 6 and 9^{o}C. The regression coefficient b, the slope of the line, which represents net efficiency, was fairly constant and seemed not to decrease with increasing size. This is in contradiction of the findings of Jones and Hislop (1978) and Jobling (1982).

Jones and Hislop (1978) found no detectable changes in net efficiency values for cod between 100 and 900 g, values varied around 0.3, while smaller fish of 5 - 40 g weight exhibited larger net efficiencies of 0.45 - 0.65. The present result showed higher slope values (0.42 - 0.61) largely depending on the high caloric values of the cod (1.71 kcal/g) used in the study. A caloric value of 1 kcal/g would have given a net efficiency value of 0.34. Minor variations between the two series can possibly be explained by the differences in diet, temperature, light conditions etc.

Most experiments were carried out with groups of fish but similar results were found for single fish. A considerable scatter of points existed and the growth rate for the maximum ration (Rmax) could not be defined. Equally scattered data were presented by Hatanka and Takashaski (1960) for mackerel, Brocksen and Cole (1972) for bardiella, corvina and sargo and Jones and Hislop (1978) for cod. All derived a linear expression between G and R. A linear relationship has also been described for various species (Birkett, 1969; Staples and Nomura, 1976; Stirling, 1976; MacLeod, 1978; Flowerdew and Grove, 1980; Jobling, 1982).

A curvlinear response could be expected in accordance with Brett (1979), Huisman (1976) and others particularly at high feeding levels. Several possibilities can explain the lack of a downward response of growth when ration levels increase to satiation or above. The use of groups of fish tends to smooth out differences. However, Jones and Hislop (1978) used only single gadoids, and found the relationship approximately linear. Secondly, present feeding techniques made it difficult to feed maximum rations, and cod in general seemed to accept larger meals at longer feeding intervals than salmonids. Such a difference in feeding behaviour could explain the difference in the shape of the G-R curves between salmonids and gadoids.

When feeding was changed from a high to a low level or vice versa, the fish did not always respond with the expected change in growth. Growth in length was recorded without feeding for many weeks. Ricker (1979) assumes that the growth process, such as cell division, probably have a certain momentum and do not stop immediately when the ration is suddenly lowered. The fish may continue to grow both in length and weight by increasing their water content.

Cod may possibly fit a linear model more closely than salmonids, although the use of a linear relationship is probably a simplification.

Maintenance requirements for cod were primarily determined in G-R experiments by calculating the food level at zero growth. The linear relationship between maintenance ration (R_m) and fish size agreed well with the data given by Jones and Hislop (1978) and Jobling (1982). A comparison between these studies are given in Table 12 for sizes between 100 and 1000 g.

TABLE 12

Comparison of maintenance ration from growth-food studies and oxygen consumption experiments.
Values in brackets are corrected to 8.5°C.

	Maintenance ration (Rm) (kcal/day)				
Weight (g)	Present[1)]	Growth-food studies Jones & Hislop,- 78[2)]		Jobling -82[3)]	Braaten, unpubl.[4]
	(6-9⁰)	(13⁰)	(8.5⁰)	(3-16⁰)	(8.5⁰)
100	0.83	1.005	(0.69)	0.97	0.71
200	1.41	1.63	(1.12)	1.79	1.25
500	2.84	3.10	(2.14)	4.01	2.66
750	3.88	4.18	(2.88)	5.72	3.71
1000	4.83	5.06	(3.49)	7.37	4.70

1) a=0.0245, b=0.765, 2) a=0.04, b=0.7, 3) a=0.017, b=0.879,
4) Oxygen consumption experiments.

The overall regression for the two experimental series were used. Similar results were also obtained by measuring routine oxygen consumption of cod at 8.4°C (Braaten, unpubl. data) using the relationship

$$y = 0.0204 \cdot W^{0.824}$$

where y represents oxygen consumption in mg O_2/h, W weight in grams and using an oxycaloric coefficient of 3.24 kcal mg of O_2 (Brett, 1979).

The cod seemed able to adjust to a maintenance level by either changing the maintenance level or increasing conversion efficiency when kept at a low feeding level for several weeks. This could explain some of the variations in the experiments and are in agreement with Brown's (1946) results on trout. The trout were able to adapt their maintenance requirements to different levels of feeding appearently due to capacity to lower the basic metabolic rate during starvation. Jones (1976) concluded that there is no one maintenance level for any fish, and that equation G = b (F - Rm) may not be valid when growth is negative.

It was further evident that growth rate decreased with increasing size and under similar environmental conditions when cod were fed to satiation. The log-log transformation gave a good linear relationship and was in agreement with similar studies on salmonids (Brett and Shelbourne, 1975) that compared and discussed results from various experiments. The slope value determined for cod of -0.45 was close to -0.41, a mean value found for three species of Pacific salmon and brook trout. This means that cod fed to satiation has a capacity to grow according to $W^{0.55}$.

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SECTION V

Genetics and disease

CHAIRMAN

N. Ryman