Growth and feeding of juvenile cod (*Gadus morhua* L.)

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Growth and feeding of immature cod were investigated in Upper Loch Torridon (57°33′N 5°36′W), a fjordic sea loch on the west coast of Scotland. Growth was estimated from mean length and weight at age, and also from the changes in length of tagged fish. Feeding rates were measured by two independent methods: 1) laboratory measurements of the ration levels necessary to produce growth rates similar to those observed in the wild (measured from mean length at age), and 2) examination of the stomach contents of wild fish, by the application of experimentally measured elimination coefficients.

Growth rates measured from mean length at age were lower than those measured from tagged fish, perhaps because faster-growing fish leave the loch, biasing mean length at age downwards. There were strong seasonal differences in the growth and condition factor of the cod, both being highest in summer and autumn and lower during winter and spring. The feeding rates estimated by the two independent methods were similar, though those estimated from growth rates were generally lower, probably reflecting an underestimation of growth rate and also differences in the diet and activity levels of laboratory and wild fish. It is suggested that the poor condition and lower food intake of fish in the winter result from a lack of vulnerable prey organisms, rather than any drop in growth efficiency at lower temperatures. The production of juvenile cod in Scottish sea lochs may well be limited by the winter food supply.

Introduction

The cod is a widely distributed marine fish, found throughout the shelf areas of the North Atlantic. Juvenile cod are often encountered close inshore, and are found in large numbers at the margins of many of the sea lochs, which are a feature of the west coast of Scotland. Our own studies in Upper Loch Torridon (57°33′N 5°36′W) have shown that the young cod settle in the shallower parts of the loch in their first year of life, when they are between 5 and 20 cm in length, and may remain there until they are over 3 years old, and almost 50 cm in length. The older fish leaving the loch are presumed to join the adult stock offshore. Acoustic tracking of individuals in the size range 30 to 40 cm has shown that at least some of the fish within the loch occupy home ranges, which are generally about one hectare in extent (Hawkins *et al.*, 1980).

Little is known of the general biology of juvenile cod in inshore waters. These fish fall below the minimum landing size for commercial catches, which are mainly taken offshore because of the imposition of fishing limits to protect the young fish. Moreover, the codling are commonly found in areas with a dense covering of benthic macrophytes, where they cannot readily be fished.

We have recently investigated the biology of cod in Loch Torridon. Our intention was to look at the factors influencing the growth and production of the young fish, and particularly to investigate the relationship between growth and feeding. The growth of fish within the population was determined by two independent methods. First, growth curves were constructed from the mean lengths and weights of fish of differing ages. Age was determined by reading the otoliths, a method which has been found satisfactory for cod (Trout, 1957; Daan, 1974). Secondly, since otolith reading is based on the subjective interpretation of visible patterns, we measured growth independently by noting changes in the length of fish which had been tagged, released, and recaptured. Such tags appear to have no adverse effect upon the growth of cod (Kohler, 1963; Jensen, 1967), though they may make the fish more vulnerable to predators.

Feeding rates were estimated by feeding fish at different ration levels in the laboratory and determining the food intake corresponding to the growth rates measured for fish in the wild. This method involves several assumptions, perhaps the most important being that the proportion of the food intake devoted to growth is similar for fish in the laboratory and in the wild. Independent estimates were obtained, for comparison, by examining the stomach contents of fish in the loch and ap-

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plying experimentally determined gastric evacuation rates for different food items to calculate the rate of food ingestion (Jones, 1974).

Growth of fish in Loch Torridon

Fish capture

The fish examined were caught with hand lines and baited hooks in Inner Loch Torridon. This fishing method can be expected to be size selective, and very small fish may not be adequately represented. Other fishing methods were tried, including gillnets, baited traps, purse seines, and towed nets, but were found to be impracticable because of dense weed cover. Fish were caught in all months of the year during the years 1974 to 1979.

The baited hook catches showed a marked seasonal variation. Catch per unit effort (c.p.u.e., in terms of fish per man per hour), summed on a monthly basis over a 6-year period from 1974 to 1979, reached a minimum in the months March, April, and a maximum in October, November. These data are presented in Figure 1, together with spot readings of sea temperature at a depth of 10 metres in Loch Torridon taken over an 8-year period. The changes in c.p.u.e. lag behind those in sea temperature by one to two months.

Determination of growth rates

During the years 1974 to 1979, 1284 captured cod were chosen at random, and their lengths (L) measured as the maximum distance between the snout and the tip of the tail, rounded up to the nearest centimetre. The stomach, liver, and intestines of most of the fish were then removed and the gutted weight (W_g) recorded to the nearest gram. The gonads were examined and weighed to the nearest 0·1 g. The stomachs were preserved in 10 % formalin and retained for later analysis. The age of the fish was then estimated by recording the annual growth zones on the saccular otolith. The otoliths were broken mid-way along their length, the exposed cross-section coated with terpineol, and the otolith viewed with strong side lighting (Trout, 1957). The incidence of opaque, outer, summer zones on the otoliths of fish was highest in July, August, and September, coinciding with the sea temperature maximum, and lowest in January, February, and March, the coldest part of the year, when they were replaced by hyaline winter zones (Fig. 1). From the pattern of zones and the time of capture the age of the fish was determined, in quarter years, assuming a birth date of 1 March (the assumed time of spawning). Thus, a fish caught in September without a winter hyaline zone was taken to be 6 months (2 quarters) old, while a fish caught at the same time and bearing a single hyaline zone was taken to be 18
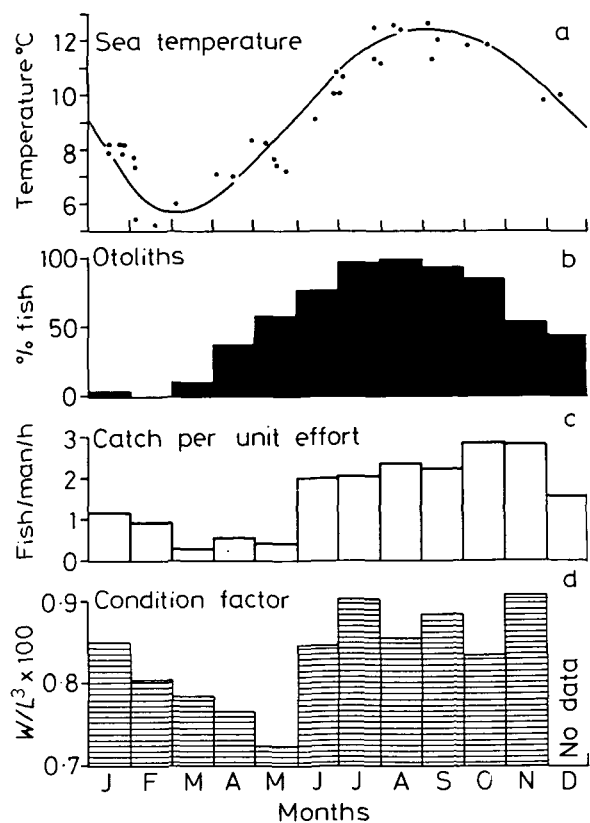

Figure 1. Seasonal changes in the growth, catch per unit effort (c.p.u.e.), and condition factor of juvenile cod in Loch Torridon, in relation to sea temperature. (a) Temperature readings taken at 10 m depth in Inner Loch Torridon throughout the period 1974–1981. A curve has been fitted by eye. (b) Percentage of fish captured in each month which show an opaque outer zone to the saccular otolith, indicating growth. (c) c.p.u.e., measured as the average number of cod caught per man-hour fished, for each month. (d) Condition factor for each month, defined in the text.

months (6 quarters) old, and so on. The mean length of fish at different ages could then be calculated and average growth rates determined for the population.

Growth with age

Figure 2 shows scatter diagrams for both length and weight against age of juvenile fish and illustrates the wide variation in growth rate within the loch. The growth in length with age followed an approximately straight line relationship, and a linear regression was fitted to the data, the equation being:

$$y = 8·45 + 0·029 \, x$$
$$(df = 1264; \; r = 0·800; \; P < 0·001)$$

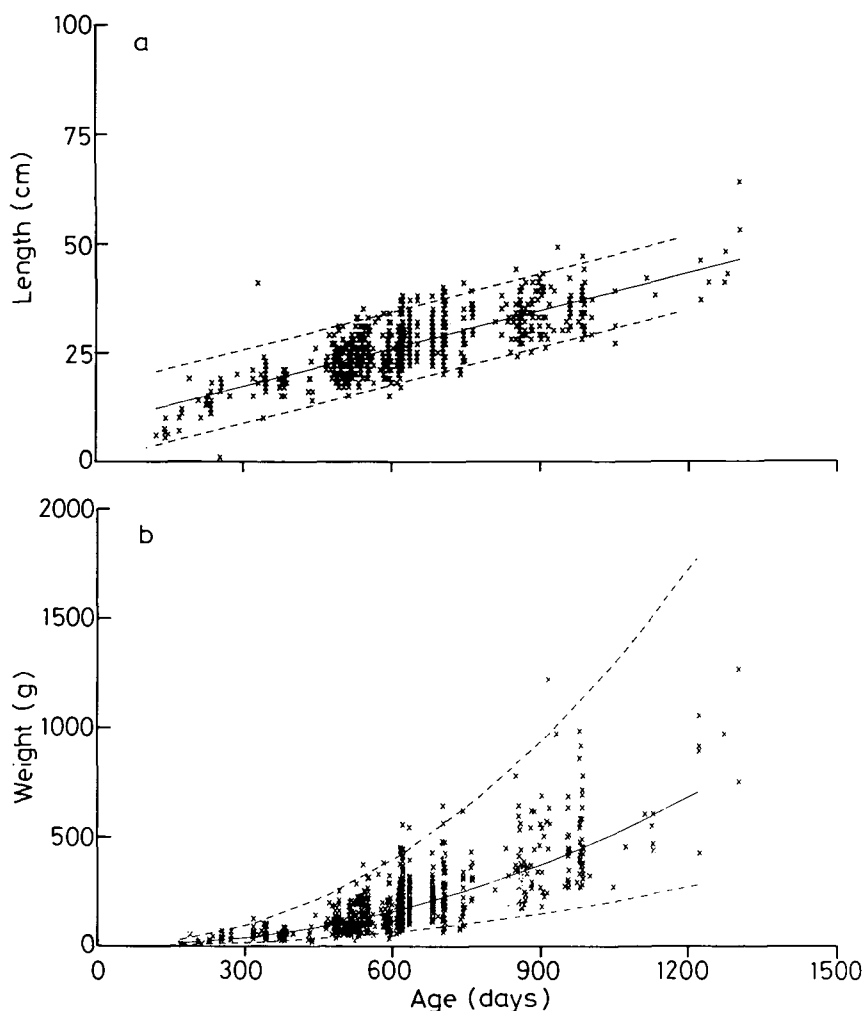where y is the length (cm) and x the age (days). The line

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Figure 2. The growth of juvenile cod in Loch Torridon. (a) Length at age. (b) Gutted weight at age. In both cases age is determined from an examination of the saccular otolith, assuming a birth date of 1 March. The lines were fitted by least squares regression, and 95 % confidence limits are indicated.

fits the data well, though it overestimates the length of the youngest fish.

The growth in gutted weight followed a linear relationship when both weight and age were transformed to logarithms, giving:

$$\log y = -3\cdot41 + 2.01 \log x$$
$$(df = 857; r = 0\cdot730; P < 0\cdot001).$$

Regressions of both length and weight against age were compared for male and female fish. With growth expressed as length no differences were observed between the two sexes. With growth expressed as weight the slopes were similar though the y intercepts differed significantly (t = 2·598; df = 967; P < 0·005). From this comparison we decided that separate analysis of the two sexes was not justified.

The growth of the young fish is also illustrated in Fig-

ure 3, which plots the length frequency distributions for fish of different ages, during different quarters of the year. There are no fish less than 3 months old nor fish older than 3 years 9 months. Diving observations show that the smallest fish cannot readily be caught with baited hooks, and that they are present in far greater numbers than the catches indicate. It is not clear whether the cod enter the loch as young fish or as eggs and larvae. The absence of older fish from the catch almost certainly indicates their real absence from the study area. Such fish can be caught elsewhere by the same fishing method.

Table 1 presents the mean length at age, and mean weight at age data for fish sampled between 1974 and 1979, expressed per quarter year of life. Figure 4 shows the mean length at age, together with the linear regression line (a = 6·24; b = 2·69; r = 0·99; df = 12; P < 0·001). In view of the very good fit of the regression
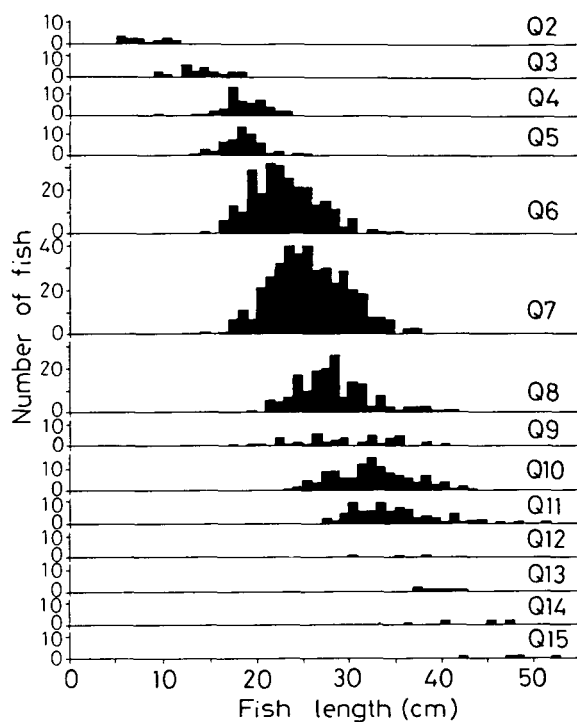
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Figure 3. The length distribution of cod of differing ages caught on baited hooks in Loch Torridon. The ages are grouped into quarter years. Note the scarcity of very small and very large fish.
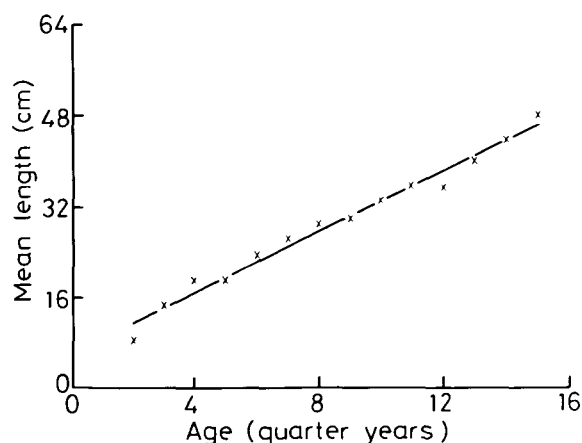

Figure 4. The mean length at age of juvenile cod in Loch Torridon. Each point represents the arithmetic mean of all cod of a given age. The line was fitted by least squares regression.

line we see no advantage in fitting more sophisticated statistical models. It is clear that the von Bertalanffy curve (Beverton and Holt, 1957), with its prediction of asymptotic growth, does not apply over this restricted

age range. However, although there is a strong linear relationship between length and age for the study population, Figure 4 does suggest that there is a cyclical pattern, with a period of about one year, superimposed upon the main trend. In Figure 5, growth is plotted as specific growth rate for both length and weight, calculated as follows:

$G_w = (\ln W_2 - \ln W_1) \times t^{-1} \times 100$ percentage weight per day where W_1 and W_2 were the initial and final weights (g), respectively; and t was the time (days), and $G_L = (\ln L_2 - \ln L_1) \times t^{-1} \times 100$ percentage length per day where L_1 and L_2 were the initial and final lengths (cm), respectively.

Table 1. Mean length at age and mean weight at age for juvenile cod captured on baited hooks in Loch Torridon. Specific growth rates are calculated as described in the text. A fish aged 1 quarter year is less than 3 months old, one aged 2 quarter years is between 3 and 6 months old, and so on.

| Age (quarter years)	Mean length (cm)	s.d.	Sample no.	Specific growth rate (% length per day) (G_L)	Mean gutted weight (g)	s.d.	Mean live weight (g)	Sample no.	Specific growth rate (% live weight per day) (G_w)
1	–	–	–	–	–	–	·	–	–
2	8·5	2·28	18	–	4·8	2·42	3·6	5	–
3	14·8	2·85	32	0·606	35·4	15·17	37·8	23	2·580
4	19·1	2·57	49	0·286	60·7	25·20	66·1	46	0·614
5	19·1	2·33	53	−0·004	56·6	20·77	61·5	50	−0·079
6	23·6	3·69	261	0·233	123·8	63·78	136·6	224	0·877
7	26·3	4·23	401	0·121	184·4	96·89	204·3	393	0·442
8	29·0	4·16	171	0·106	235·2	104·07	261·1	147	0·270
9	30·0	5·42	46	0·036	250·0	131·52	277·6	40	0·067
10	33·3	4·77	124	0·117	370·9	181·15	412·7	78	0·436
11	35·6	4·94	87	0·073	462·2	196·59	514·7	84	0·243
12	35·3	4·04	3	−0·009	377·0	95·40	419·5	3	−0·225
13	40·1	1·95	7	0·140	566·1	93·81	630·8	7	0·448
14	43·9	4·22	7	0·097	775·3	239·28	864·5	7	0·346
15	48·3	4·11	4	0·105	1007·7	365·15	1124·2	2	0·289

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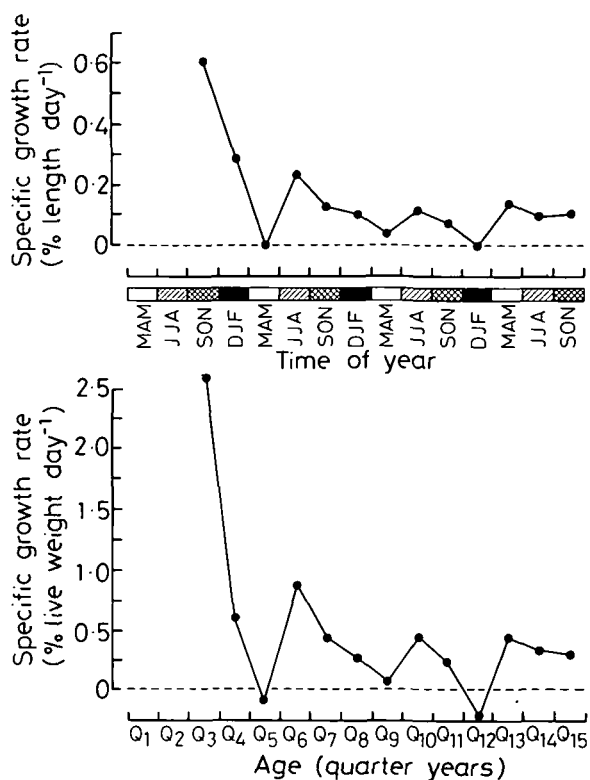
Figure 5. The specific growth rate of juvenile cod with age in Loch Torridon. (Top) Growth in length. (Bottom) Growth in live weight. Points represent the specific growth rates of juvenile cod calculated from the mean length and weight at age. Seasons of the year are indicated by the repeating pattern shown between the graphs, e.g., Q_1, Q_5, Q_9, and Q_{13} represent the period March/April/May.

The data in Figure 5 are grouped both by age and by season. The patterns for both length and weight are similar, with minimum values of specific growth rate during March, April, May, rising to a peak later in the year. The winter minimum occurred earlier for older fish (during December, January, February) though fewer of these were sampled (Table 1).

Length and weight

The relationship between length and gutted weight for the fish is shown in Figure 6. A line was fitted to the logarithms of both sets of data by least squares regression (a = $-2\cdot218$; b = $3\cdot121$; r = $0\cdot932$; df = 1123; P < 0·001). Several authors have pointed out that the least squares method is not the best way to examine the length−weight relationship (Ricker, 1973; Laws and Archie, 1981). However, when the relationship between the two variables is very significant, as it is here,

then the result obtained is little different from that obtained by other methods. Gutted weight was chosen for these measurements to avoid introducing variation through differences in the weight of food inside individual fish. The relationship between gutted weight and live weight was established by measurements on a sample of the fish with empty stomachs, a straight line being fitted by least squares regression (a = 1·54; b = 0·895; df = 24; r = 0·999; P < 0·001).

The condition factor (CF) of the individual fish was calculated as

$$CF = W_g \, L^{-3} \times 100.$$

Though the Torridon data showed an exponent relating weight and length which was significantly different from 3 (b = 3·121, P < 0·05), the equation was left unchanged to allow easier comparison with data from other sources.

Condition factor varied with the time of the year, as shown in Figure 1, the lowest values in May indicating that fish were in poorest condition at the end of their period of low growth, just after the winter period of low temperature (Fig. 5). There was a pronounced increase in condition factor in June, the high level being maintained until November.

Growth in the sea

The growth of the young cod in offshore areas to the west of Scotland had not been examined. However, good data are available for the east coast, derived from the ICES Young Fish Surveys, conducted with small-mesh trawls in the North Sea during 1981 and 1982, and weighted by area, size, and catch rates. Mean lengths at
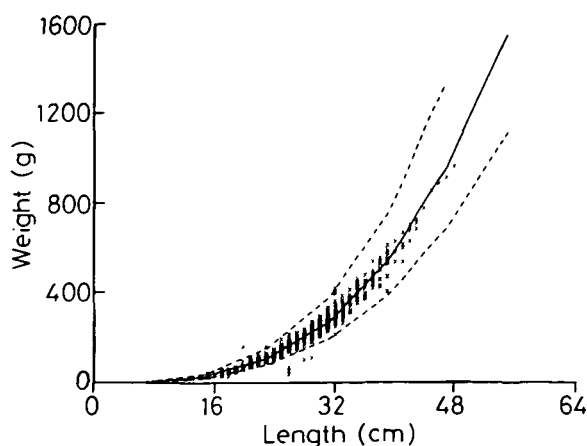

Figure 6. The relationship between gutted weight and length for juvenile cod caught on baited hooks in Loch Torridon. The line was fitted by least squares regression, and 95 % confidence limits are indicated.

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Table 2. Mean length at age of Loch Torridon fish compared with that of North Sea fish. The North Sea data are taken from ICES Young Fish Surveys with a small-mesh trawl, conducted in February. The Torridon fish are taken from Jan/Feb/Mar catches on baited hooks. The ages of the Torridon fish are adjusted to conform to those of the North Sea fish (assuming a birth date of 1 January).

Age (years)	Mean length (cm)				
	Torridon	ICES 1981		ICES 1982	
		Male	Female	Male	Female
0	–	–	–	–	–
1	19·1	20·1	20·6	20.6	20·7
2	29·0	30·4	30·4	36·5	37·2
3	35·3	52·9	53·0	50·2	50·2
4	>48·3	71·3	70·6	70·5	70·2

age for these fish are presented in Table 2. The ages shown for the Torridon fish in this table have been adjusted to conform to the ages of the North Sea fish (which assume a birth date of 1 January). The data from the North Sea are obtained from surveys conducted in February, and the Torridon data selected for comparison are taken from fish captured in the same period. There are clear differences between the sets of data. Though the offshore and Torridon fish show similar mean length at age in the first year, the offshore fish show much greater mean length in subsequent years.

Growth of tagged fish in the loch

In the years 1974 to 1978, 1828 cod were captured and tagged in Loch Torridon. The majority were tagged with yellow spaghetti tags, though in the early years some carried orange flag tags, and others green plastic smolt tags. Both of the latter types of tag became fouled with algae and were more readily shed, and their use was discontinued. The fish were measured to the nearest cm above, tagged, and released immediately, usually close to the site of capture; 236 of the tagged fish were subsequently recaptured. Of the recaptures 37 were discarded because the length of the fish was not recorded, leaving 199 pairs of data from which growth rates could be calculated. Several fish showed a slight decrease in length, usually after a very short period in the sea, presumably because of inaccuracies in measurement. Measurement errors are likely to be present and remain undetected throughout the rest of the data, however, and the negative values were not discarded as this would have introduced bias into the results.

Figure 7 shows a scatter diagram of the length increment in centimetres against the time the fish were free in days. The line of best fit was calculated by the least squares regression (b = 0·042; a = −0·447; r = 0·912; df = 197; P < 0·001). Most recaptures were made very soon after release. To test whether these fish significantly affected the results the regression was recalculated using only fish caught more than 100 days after re-
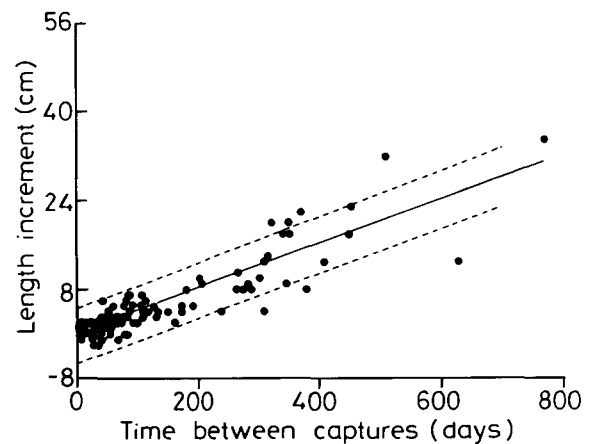

Figure 7. The growth rate of juvenile cod in Loch Torridon, as estimated from tag and recapture data. The length increments for cod which were tagged and subsequently recaptured are plotted against the number of days between release and recapture. The line was fitted by least squares regression, and 95 % confidence limits are indicated.

lease. The slopes of the two regressions were not significantly different.

The slope of the regression calculated from the complete tagging data was significantly steeper than the slope of the regression obtained from the length at age data, shown in Figure 2 (t = 5·64; df = 1461; P < 0·001), indicating a faster growth rate for the tagged fish. The larger fish in a given age class may leave the loch earlier, and their departure may cause the mean length at age data to provide an underestimate of the actual growth rate. It is also probable that smaller fish in the younger age classes were not sampled representatively, leading to a further underestimation of the growth rate.

Gonad development

The sex of 963 of the sampled fish was determined, and maturation stage assessed using the table described by

Table 3. Sexual maturation of juvenile cod in Loch Torridon. Maturation stages are given for fish of differing age, and were derived from descriptions by West (1970).

	Male Age					Female Age				
	0	1	2	3	Total	0	1	2	3	Total
Maturation stage										
I	11	297	75	3	386	29	354	44	2	429
II	7	7	16	3	33	0	47	47	5	99
III	0	2	5	0	7	0	1	4	1	6
IV	0	1	0	0	1	0	0	0	0	0
V	0	1	0	0	1	0	0	0	0	0
VI	0	0	0	0	0	0	0	1	0	1
Mean GSI	0·000	0·035	0·055	0·088	–	0·098	0·099	0·276	1·75	–

Average Gonadosomatic Index for fish of differing age: Males

Age quarter	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Mean GSI....	–	–	0·000	0·000	0·000	0·002	0·011	0·130	0·000	0·020	0·113	0·000	0·000	0·065	0·267

Average Gonadosomatic Index for fish of differing age: Females

Age quarter	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
Mean GSI....	–	–	0·000	0·124	0·000	0·090	0·108	0·120	0·111	0·446	0·271	0·309	2·760	0·491	0·482

West (1970). The gonads were weighed, and a gonadosomatic index (GSI) calculated for each individual

$$GSI = \text{gonad weight} \times W_g^{-1} \times 100.$$

The numbers of fish of differing maturity stage are listed in Table 3, where mean values of GSI are also presented for fish of differing age. The great majority were virgin fish at a very early gonad maturation stage. Only a single fish, a female 40 cm in length, caught in March, was ripe and in spawning state. Gonad weights constituted less than 1 % of the body weight for male fish, and less than 2 % for female fish. These compare with values of between 3·5 and 16 % for fully ripe males, and between 4 and 23 % for corresponding females (West, 1970). Thus, cod seem to leave Upper Loch Torridon before they are mature. There is no strong indication of a seasonal variation in the GSI values for the immature fish (Table 3).

Laboratory studies of growth and ration

Feeding experiments in the laboratory

Fish caught with hand lines in shallow water at Loch Torridon were transported to the Marine Laboratory and kept in large rectangular tanks (1·65 m³), supplied with recirculated water from a large reservoir. They were acclimated to appropriate experimental temperatures at a rate of 1°C change per day, and then main-

tained at the final temperature for at least four weeks before experiments began. During acclimation the fish were fed ad libitum three times per week.

The fish were divided into three size classes (viz. class 1, 16·0 to 23·0 cm; class 2, 23·5 to 30·0 cm; and class 3, 30·5 to 40·0 cm). The growth of all three size classes was studied at 10°C (range 9° to 11°), classes 1 and 2 were also studied at 15°C (range 14° to 16°), and class 2 at 7°C (range 6·5° to 8°) and 18°C (range 16·5° to 18·5°). The numbers of fish in each experiment varied between 9 and 15.

The selected fish were carefully transferred to smaller rectangular tanks divided up with netting partitions. Each fish was separately confined to a compartment approximately 60 × 35 × 30 cm, and allowed to remain there undisturbed, except for feeding, for one week before experiments began. To investigate the effects of close confinement a separate experiment was run with class 2 fish at 10°C. Six fish were kept in much larger individual compartments (189 × 42 × 69 cm) within a large tank, but were otherwise treated similarly to those kept in close confinement. All the fish examined remained fairly quiescent within their pens, and rarely swam actively.

The fish were fed every two days on specially formulated pellets, made up from a mixture of the four major components of the natural diet in Loch Torridon, viz. polychaetes, molluscs, crustaceans, and fish. The proportion of each item at a particular temperature was determined by taking the mean percentage weight of

Table 4. Composition of the diet in experiments at different temperatures, shown as percentage of the wet weight before freeze drying. Calorific values are expressed in terms of kJ/g ash-free dry weight. The water content is expressed as a percentage of the total wet weight of diet, and the ash content as a percentage of the total dry weight of diet.

Components	Temperature (°C)			
	7	10	15	18
Fish (*Ammodytes,*				
Limanda, Merlangius) .	47	37	45	40
Crustaceans (*Carcinus,*				
Pagurus, Pandalus)....	30	28	26	25
Molluscs (*Buccinum,*				
Littorina)	23	15	17	17
Polychaetes (*Nereis,*				
Arenicola)	–	20	12	18
Calorific value	22·64	25·24	23·49	23·45
	±0·67	±1·17	±1·01	±0·75
Water content	27	25	27	28
Ash content	24	29	26	30

each item found in the stomachs of cod at the appropriate time of year, and weighting this with an experimentally determined elimination coefficient (Jones, 1974). The appropriate items were not always available, and on occasions other natural materials were substituted. Table 4 gives the composition of the diet at different temperatures. To manufacture the diet the different components were freeze dried, milled to a fine powder, mixed with edifas (a cellulose binder of known calorific value, which we assumed was not digested by the cod) and a known quantity of water, and extruded as moist pellets. The pellets were kept in a deep freeze before being presented to the fish. Water content was checked regularly and showed negligible change. Calorific values of the samples were determined by bomb calorimetry using a Phillipson Microbomb Calorimeter (Gentry and Weigert's modification of the one described by Phillipson, 1964). A correction was introduced for the undigested edifas. Proximate analysis showed the diet to be high in protein and mineral content but low in carbohydrate and lipid (Table 5). Though this diet had approximately the same composition and energy content as the natural food of cod, it is likely that it was more rapidly digested, because of the grinding and freeze drying to which it had been subjected.

In each of the experiments the fish were not fed for two days to minimize the weight of food in the stomach. They were then anaesthetized with benzocaine (7 : 100 000 ethyl *p*-amino benzoic acid in water), weighed to the nearest 0·1 g and measured to the nearest 0·5 cm. To avoid disturbing the fish the anaesthesia was performed within the holding tank. Subsequently, the fish were returned to fresh aerated seawater in the same tank. Feeding commenced 24 hours after the measurements. The fish were fed pre-weighed rations of pellets every second day. The food proved to be palatable to the fish, and was often taken avidly. At the end of the

experiment the total intake of pellets was calculated, and divided by the duration of the experiment to give the daily ration.

Each experiment lasted from 45 to 75 days, the length and weight of each fish being recorded under anaesthesia every two weeks. At the end of the experiments the fish were killed by a sharp blow to the head, and then freeze dried for subsequent analysis.

Growth and ration

The growth of fish fed at different ration levels in the laboratory was derived as a daily increase or decrease in live weight, expressed in terms of specific growth to minimize effects arising from size differences. Daily ration levels were calculated in terms of the equivalent wet weight of natural food composing the diet, expressed as a percentage of the initial body weight.

Figure 8 shows the relationship between specific growth in weight and ration level for different size classes at different temperatures. There is no evidence of growth tailing off at high ration levels, as has been suggested for feeding experiments with other fish (Brett *et al.*, 1969). Condrey (1982) has recently reviewed published data on growth/ration relationships in fish and has concluded that there is more often a linear relationship between growth and ingestion.

The equations of the fitted straight lines are tabulated in Table 6. The relationship between specific growth rate and ration level was highly significant ($P < 0.001$) for all size classes, at all temperatures. The regressions were compared and it was found that though their slopes did not differ significantly ($P > 0.05$), their intercept values on the y axis were significantly different (P between 0·02 and 0·001). The seven sets of data were fitted with a pooled slope of 0·1905 (s.e. = 0·0082), yielding the intercept values given in Table 7.

There is little evidence from these new intercept values that the size of the fish had an important influence

Table 5. Chemical composition of the diet for the growth experiments at 15°C. Values are expressed as a percentage of the wet pellet weight, except for the ash content, which is expressed as a percentage of dry weight.

Constituents	Percentage by weight
Crude protein[a]	43·30
Crude oil[b]	3·70
Available carbohydrate[c]	3·01
Water content	26·97
Ash content	24·02

[a] Kjeldahl, N × 6·25.
[b] Chloroform : methanol extraction, charring method with H_2SO_4, and colorimetric assay (Marsh and Weinstein, 1966).
[c] Anthrone method (Strickland and Parsons, 1972).

Table 6. Regression equations for specific growth rate (y, % live wt day^{-1}) against ration level (x, in terms of equivalent wet weight of food organisms ingested, expressed as a percentage of body weight per day) for different size classes of juvenile cod at different temperatures.

Temperature (°C)	Size class	Mean weight (g)	Regression equation y = bx + a		r	df	P
			a	b			
7	2	206	−0·0520	0·1894	0.840	13	<0·0005
10	1	91	−0·0623	0·1779	0·945	8	<0·0005
10	2	195	−0·0967	0·2099	0·949	11	<0·0005
10	3	397	−0·1939	0·2428	0·883	13	<0·0005
15	1	70	−0·1625	0·1849	0·953	13	<0·0005
15	2	129	−0·1274	0·1782	0·970	7	<0·0005
18	2	166	−0·3085	0·2048	0·968	10	<0·0005

upon the relationship between specific growth and percentage ration. Figure 9 shows fish of different size classes on a single plot for two different temperatures. The lack of any size effect almost certainly reflects the small range of sizes examined. It is well established that there is a decline in both gross and net conversion efficiency with increasing body size for fish if the whole range of possible body sizes is considered (Brett, 1970;
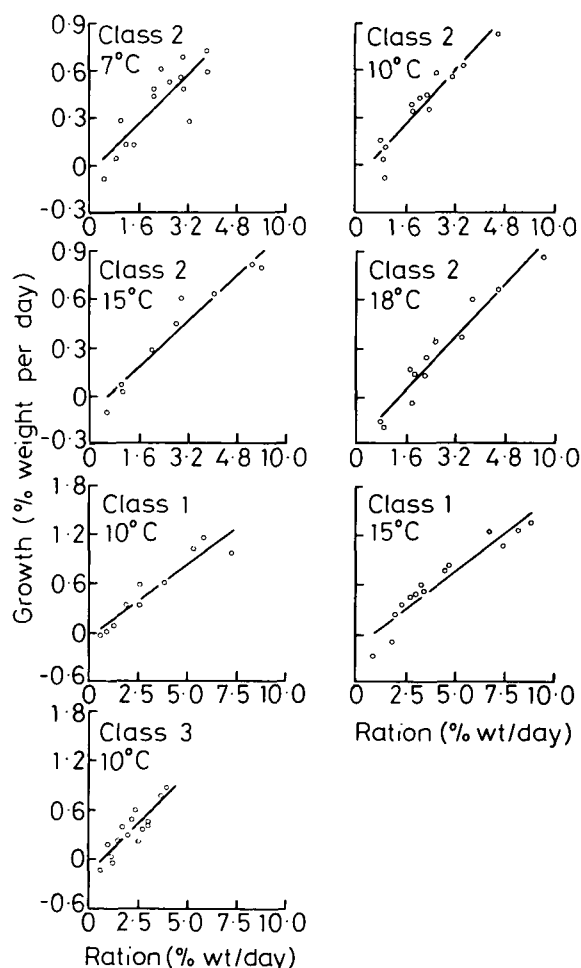

Table 7. Values of the y intercept calculated for each temperature, using the slope of 0·1905 (s.e. 0·0082) for the pooled data.

Size class	Temperature (°C)	y intercept
2	18	−0·2693
1	15	−0·1860
2	15	−0·1627
1	10	−0·1026
3	10	−0·0784
2	10	−0·0551
2	7	−0·0541

Jones and Hislop, 1978). The term "gross conversion efficiency" refers to the increase in body weight of fish divided by the quantity of food consumed (Ivlev, 1945; Paloheimo and Dickie, 1966). The term "net conversion efficiency" refers to the increase in body weight of fish divided by the quantity of food consumed exclusive of maintenance requirements (Brown, 1957), or to the slope of the regression line relating growth rate to food intake (Jones and Hislop, 1978).

It was clear that temperature did have a significant effect, the specific growth rates for a given ration level being greatest at the lowest temperature. A single relationship was derived for each temperature regardless of fish size by taking the pooled slope (b = 0·1905) and fitting the best regression line to the data. The regression equations are presented in Table 8. From these equations we have calculated the values of ration corresponding to zero growth, that is, the maintenance ration.

The values are given in Table 8 together with the calculated confidence limits. The higher the water temper-

Figure 8. The relationship between specific growth in weight (G$_w$) and ration level for different size classes of cod at different temperatures in laboratory feeding experiments. Each point represents data from an individual fish. The ration is given in terms of the equivalent wet weight of food, expressed as a percentage of fish weight per day. The line is fitted by least squares regression. Temperature and size class are indicated for each graph.
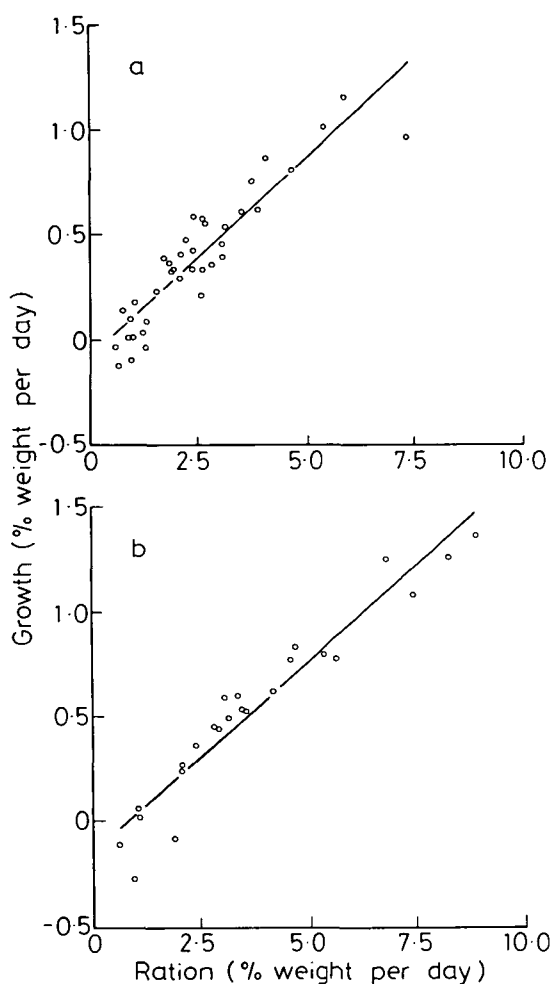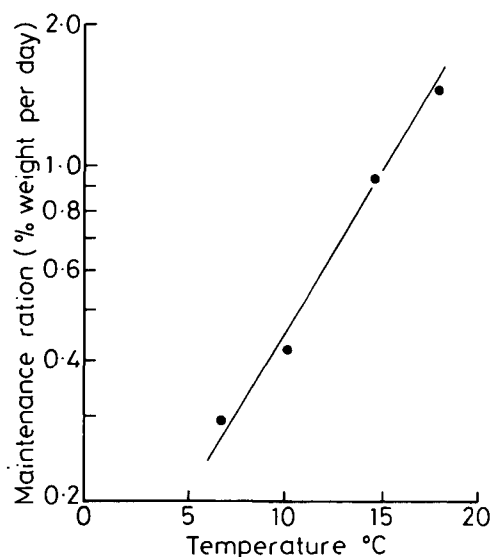
Figure 10. The influence of temperature upon the maintenance ration for cod estimated from laboratory feeding experiments. The maintenance ration is given in terms of the equivalent wet weight of food, expressed as a percentage of fish weight per day. Each point represents the x intercept of a regression between growth rate and ration level for a given temperature, all size classes combined. The line was fitted to the log of maintenance ration by least squares regression.

Figure 9. The relationship between specific growth in weight (G_w) and ration level for cod in laboratory feeding experiments. All size classes of cod have been combined. The ration is given in terms of the equivalent wet weight of food, expressed as a percentage of fish weight per day. (a) Relationship at 10°C. (b) Relationship at 15°C.

ature, the larger the maintenance ration required by the juvenile cod. Though the maintenance rations at 7°C and 10°C were not significantly different, the value at

15°C was significantly different from those at 10° and 18°C, and the value at 18°C was significantly different from those at all other temperatures tested. The effect of temperature upon the maintenance ration is shown in Figure 10, where the maintenance ration (C_m expressed as wet weight of food as a percentage of body weight per day) is plotted on a logarithmic scale against temperature (T°C). This relationship was found to be linear, the equation being

$$\log C_m = 0.065T - 1.018$$
$$(df = 2; r = 0.998; P < 0.002).$$

This effect of a rise in temperature upon the maintenance ration is well known for fish. Most of the energy provided by the maintenance ration is expended as standard metabolism (Averett, 1969; Niimi and Beam-

Table 8. Regression equations for specific growth in weight (y, % live wt day^{-1}) against ration level (x, in terms of equivalent wet weight of food organisms ingested, expressed as a percentage of body weight per day) at each temperature. The equations are derived for a common slope of 0·1905. The maintenance rations, and their 95 % confidence limits, are given for each temperature.

Temperature (°C)	Regression equation y = a + bx		Maintenance ration (% W day^{-1})	Confidence limits
	a	b		
7	−0·0541	0·1905	0·284	0·000−0·648
10	−0·0768	0·1905	0.403	0·112−0·664
15	−0·1773	0·1905	0·931	0·549−1·271
18	−0·2693	0·1905	1.414	1·010−1·798

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ish, 1974), which can be expected to increase with temperature on thermodynamic grounds (Kelso, 1972; Davies and Massey, 1977). A result of the increase in the maintenance ration is a decline in the gross conversion efficiency (K_1) with temperature. Our values of K_1 for juvenile cod declined from a mean value of about 20 % (measured on a wet weight basis) at 7°C to a mean value of about 12 % at 18°C. The net conversion efficiency for cod was not significantly affected by temperature in our experiments, however.

Clearly, for cod fed at moderate ration levels growth is more efficient at lower temperatures. It should be noted, however, that the maximum growth rate for fish fed to satiation bears a different relationship to temperature. An optimum temperature of 13° to 15°C has been suggested for the growth of cod in these circumstances (Jobling, 1983). Essentially, the rate of ingestion, and hence the growth rate, reaches a maximum value for fish fed to excess, and the maximum growth rates are attained at lower ration levels for fish at lower temperatures.

Fish fed below the maintenance ration showed a reduction in weight, presumably as a result of the breakdown of body reserves. There was a trend towards a higher loss in body weight for zero rations at the higher temperatures. Growth in length of the fish increased

with ration at levels above maintenance, but was not reduced at ration levels below maintenance, resulting in a drop in the condition factor of the poorly fed fish. Figure 11 shows the relationship between final condition factor and percentage ration level for fish at different temperatures. There was a clear positive relationship at all temperatures, the condition factor being higher for fish fed at higher ration levels. The analysis of variance showed no significant differences between the slopes of the regression lines at different temperatures (P > 0·05), but the y intercepts at 7° and 10°C were significantly different from those at 15° and 18°C (P < 0·001), and the elevation at 15°C was significantly different from that at 18°C (P < 0·05).

The higher growth rate of well-fed fish was accompanied by a higher energy content in terms of kJ per gram ash-free dry weight of the whole fish carcass (Fig. 12 a), and by a lower water content (Fig. 12 b), indicating changes in the fat and protein content (Brett et al., 1969; Pandian, 1970; Love, 1980). Regression analysis between ration size and final calorific content, and ration size and final water content, showed that both relationships were significant (a = 22·151; b = 0·214; r = 0·642; df = 62; P < 0·001 and a = 82·372; b = −0·385; r = 0·570; df = 71; P < 0·001 respectively).
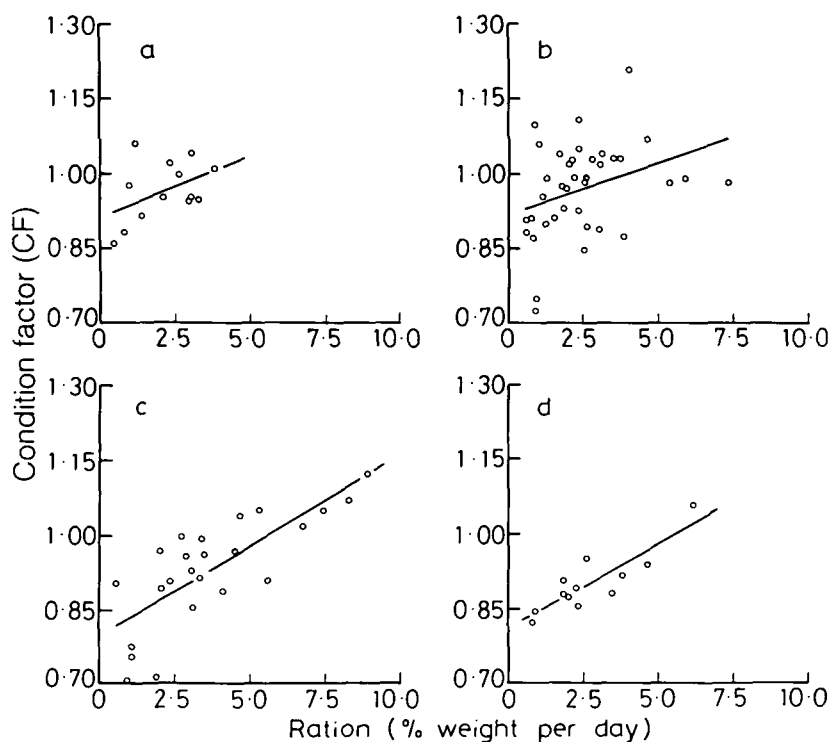
There was no evidence of sexual maturation in any of

Figure 11. The relationship between ration level and condition factor (CF) for cod at four different temperatures, derived from laboratory feeding experiments. The ration level is given in terms of the equivalent wet weight of food, expressed as a percentage of fish weight per day. All size classes have been combined. The lines were fitted by least squares regression. (a) 7°C; (b) 10°C; (c) 15°C; (d) 18°C.
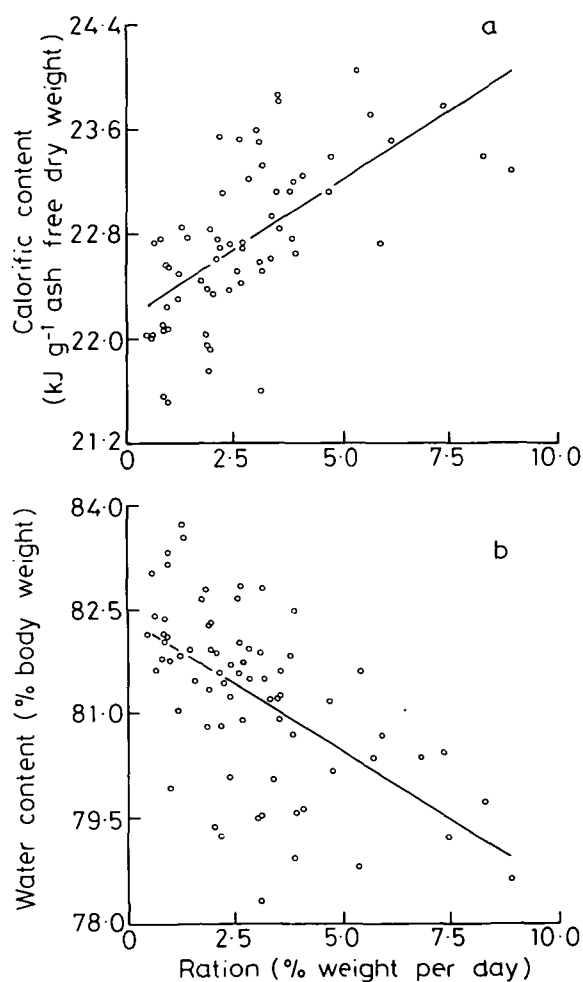
Figure 12. The influence of ration level on the body composition of juvenile cod in laboratory feeding experiments. The ration level is given in terms of the equivalent wet weight of food, expressed as a percentage of fish weight per day. Each point represents the data from a single fish. All size classes and temperatures have been combined. The lines were fitted by least squares regression. (a) Ration and calorific content. (b) Ration and water content.

ences were not significant. We have therefore assumed that our experimental growth rates were not unduly influenced by the close confinement of the fish.

In analysing the results of the feeding experiments the ration of food consumed by the fish has been given in terms of its wet weight. In addition, however, measurements were made of the calorific content of the diet. We have confirmed that the same conclusions apply, regardless of the form in which the ration is expressed. The final regression equations for the relationship between specific growth rate (in terms of live weight) and energy intake (in kJ per day per kg body weight) are given in Table 9.

Estimation of food intake from the growth of free-living fish

Knowing the growth rates of fish in the wild, and having measured the ration levels producing particular growth rates in the laboratory, we have attempted to estimate the food intake of fish in the wild. Implicit in any such estimation is the assumption that the main energy outputs over and above growth of the body, are similar for fish in the sea and in the laboratory. Juvenile cod in Loch Torridon are not highly active fish (Hawkins et al., 1980). Nevertheless, the restricted space available to fish in the laboratory, and the lack of any need for the fish to search out and attack their food means that the energy they consumed in movement was minimal. Moreover, as we have already noted, the food material supplied was macerated, perhaps leading to lower food processing costs for fish in the laboratory. Both these factors would lead to higher growth for a given ration compared with fish in the wild, leading to an underestimate of the food requirements of wild fish.

the experimental fish, all gonads remaining at maturation stage I.

Two groups of fish of similar size range were kept at 10°C. The individuals in the first group, like the rest of the experimental fish, were closely confined in small individual pens. The individuals in the second group were kept in much larger pens. Comparison of the slopes and y intercepts of the regression lines of specific growth rate and ration for the two groups showed that differ-

Table 9. Regression equations for specific growth in weight (y, % live wt day^{-1}) against energy content of the ration consumed (y, kJ kg^{-1} day^{-1}), at each of the four experimental temperatures. The equations are derived for a common slope of 0·0041. The energy consumed as the maintenance ration (kJ kg^{-1} day^{-1}) and the 95 % confidence limits, are given for each temperature.

Temperature (°C)	Regression equation y = a + bx		Maintenance ration (kJ kg^{-1} day^{-1})	Confidence limits
	a	b		
7	−0·0480	0·0041	11·71	0·00−28·17
10	−0·0983	0·0041	23·98	9·70−36·41
15	−0·1479	0·0041	36·07	17·31−52·30
18	−0·2436	0·0041	59·41	39·52−77·62

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Table 10. Estimate of the daily ration consumed by juvenile cod, calculated by applying information on growth at different ration levels in the laboratory to data on the growth of fish in Loch Torridon. Data are presented for successive quarter years of life in the loch. The estimated ration is given in terms of the equivalent live weight of food organisms.

Months	Age (quarter years)	Mean length (cm)	Mean live weight (g)	Median temp. (°C)	Specific growth rate of wild fish (% live W day⁻¹)	Estimated ration (g day⁻¹)	Estimated maintenance ration (g day⁻¹)
JJA	2	8·5	3·6	11·14	–	–	–
SON	3	14·8	37·8	11·69	2·580	5·339	0·220
DJF	4	19·1	66·1	7·86	0·614	2·341	0·210
MAM	5	19·1	61·5	7·11	−0·079	(−0·078)	0·177
JJA	6	23·6	136·6	11·14	0·877	7·003	0·714
SON	7	26·3	204·3	11·69	0·442	5·929	1·189
DJF	8	29·0	261·1	7·86	0·270	4·530	0·830
MAM	9	30·0	277·6	7·11	0·067	1·777	0·799
JJA	10	33·3	412·7	11·14	0·436	11·605	2·158
SON	11	35·6	514·7	11·69	0·243	9·558	2·996
DJF	12	35·3	419·5	7·86	−0·225	(−3·620)	1·334
MAM	13	40·1	630·8	7·11	0·448	16·653	1·817
JJA	14	43·9	864·5	11·14	0·346	20·229	4·521
SON	15	48·3	1124·2	11·69	0·289	23·597	6·543

Given the data in Table 1, for mean values of G_w during the life of the juvenile fish in Loch Torridon, and knowing the median temperatures for each quarter of the year, it is possible to estimate the ration consumed by the fish for each quarter year of their lives from the growth/ration equations obtained in the laboratory. Thus, by linear interpolation between the intercepts given in Table 8, new intercept values were calculated for the appropriate temperatures in Loch Torridon, and the ration corresponding to the specific growth rate in the wild was then obtained. These values are tabulated in Table 10, and plotted later, in Figure 19. It should be noted that by deriving growth in the wild from the mean weight at age data we are likely to underestimate the food intake further, since growth measured in this way was significantly lower than that obtained from tagging data.

The most striking feature of these data is a strong seasonal variation in the estimated ration consumed, the food intake dropping almost to zero in winter/spring. It was clear from the results of the laboratory feeding experiments that the gross conversion efficiency of the fish was highest at 7°C, the maintenance requirements of the fish being quite low at this temperature. Thus, the observed fall in specific growth rate of the wild fish in winter/spring (Fig. 5), and hence in the estimated ration (Fig. 19), must be explained by a real decline in the rate at which food is consumed or by an increased energy expenditure at this time. The low growth rate is also accompanied by a steady decline in condition factor during the winter/spring (Fig. 1). There is a sudden restoration of condition factor during June/July, the period when our estimate of food intake is highest. At the same time, there may be an increase in the willingness of the fish to take bait, judging from the increase in catch per unit effort (Fig. 1).

Superimposed on this strong seasonal variation there is a trend towards increased food consumption (in terms of g per day) as the fish grow larger, though if consumption is considered as a percentage of body weight it is evident that this is highest for the smallest fish.

The food consumed by juvenile cod

Analysis of the stomach contents of free-living cod

Stomach contents were examined from a sub-sample of 911 cod, from the total of 1284 fish caught on baited hand lines within the confines of Inner Loch Torridon. Underwater television observations showed that the hooked fish did not regurgitate any food material if they were hauled rapidly to the surface soon after they were hooked and then killed immediately. Moreover, though it might be expected that baited hooks were more attractive to less-well-fed individuals, introducing a sampling bias, in practice c.p.u.e. was higher when the stomachs contained food, and lower when they were relatively empty (compare Figs. 1 and 16). Few stomachs were sufficiently full for the fish to be described as satiated by the standards applied to laboratory-fed cod. If there was any bias, it was probably in overestimating the quantities of food eaten during the winter, when the low c.p.u.e. indicated that most fish were either not available or not inclined to attack baited hooks. At that time we may only have caught and sampled fish which were feeding.

The formalin-preserved stomachs were examined after several weeks' storage. Individual food items were separated, and identified, excess moisture removed with absorbent tissue, and each item weighed. Any remaining unidentifiable material was also weighed. Indi-

gestible items were recorded separately. All weights tabulated are formalin-preserved values, unless otherwise stated.

The stomach contents

Food material was found in 85 % of the stomachs examined, the mean weight of digestible food being 2·2 g per fish. At first sight the diet of the young cod appeared to be very varied, with over 50 different prey species occurring in the stomachs sampled. The principal prey items are listed in Table 11. They include a variety of crustaceans, ranging from large crabs to the smaller prawns and shrimps, several species of marine snail, burrowing bivalves, a variety of errant and sedentary polychaete worms, several small benthic fish, sea urchins, and brittle stars, nemertine and priapulid worms. By far the most common individual species encountered was the hermit crab *Pagurus bernhardus* (L.). Material like small stones, coralline algae, gastropod shells, bait, and living nematodes were omitted in calculating the total weights of food material.

Most of the cod stomachs contained relatively few food items. The mean number of identifiable and digestible items in the stomach was 2·2 per fish, each item weighing an average of 1·0 g.

Changes in diet with size

To examine changes in diet with growth the fish were divided into different length classes and the various food organisms were grouped into several broad categories,

Table 11. The principal prey items found in the stomachs of juvenile cod at Loch Torridon. Only items found in more than 1 % of stomachs have been listed. Since many species were represented, some have been aggregated into families, or other taxonomic groups, especially where identification to the species level could not be confirmed. Only the most common individual species have been shown. The weights given are formalin-preserved weights.

Prey item	% of all fish containing item	Mean weight of item (g)
Polychaeta	13·64	0·162
Chlorhaemidae	0·99	0·006
Pectinariidae	1·21	0·012
Glyceridae	1·32	0·005
Stylaroides plumosa (Muller)	2·97	0·027
Aphrodite aculeatea L.	1·32	0·038
Echinodermata	6·16	0·059
Ophiura spp.	1·32	0·011
Ophiothrix fragilis (Abildgaard)	1·87	0·014
Psamechinus miliaris (Gmelin)	2·31	0·020
Lamellibranchiata	6·38	0·107
Solenidae	1·21	0·028
Mya arenaria L.	3·19	0·048
Gastropoda	1·65	0·014
Decapoda	61·65	1·287
Pagurus bernhardus (L.)	35·86	0·557
Macropipus depurator (L.)	4·07	0·198
M. arcuatus (Leach)	6·49	0·197
Hippolytidae	4·07	0·021
Crangonidae	3·41	0·031
Pandalidae	6·82	0·115
Vertebrata (Pisces)	15·07	0·483
Pholis gunellus (L.)	4·18	0·097
Algae	6·38	0·050
Corallina spp.	4·29	0·036
All food material, excluding indigestible items	84·82	2·222

Table 12. The main categories of prey item found in the stomachs of juvenile cod. Coefficients of elimination (Q g h^{-1}) are presented for the different food items and are given for a standard fish length of 40 cm and a standard temperature of 12°C.

| Category	Description	Q at 12°C	Authority
I	Large epibenthic decapod crustaceans, including *Pagurus* spp., *Macropipus* spp., *Carcinus, Cancer, Inachus, Galathea*, and *Munida*	0·07	Own data
II	Small crustaceans, including *Pandalus, Crangon*, amphipods, copepods, and mysids	0·19	Jones (1974)
III	Gastropods, including *Gibbula* spp., and *Buccinum*	0·20	Assumed value
IV	Lamellibranchs, including *Mytilus, Chlamys* spp., *Cardium* spp., *Ensis* spp., *Mya*, and *Spisula*	0·22	Jones (1974)
V	Polychaete worms, including *Goniada, Nereis, Aphrodite, Stylaroides*, nephthyds, nereids, chlorhaemids, pectinariids, terrebellids, and phyllodocids	0·31	Jones (1974)
VI	Fish, including young gadoids, clupeids, gobies, pleuronectids, *Pholis*, and *Spinachia*	0·26	Jones (1974), value for saithe flesh
VII	Echinoderms, including *Ophiura, Ophiothrix, Amphiura, Marthasterias, Asterias*, and *Psamechinus*	0·15	Jones (1974)
VIII	Nemertines and Priapulids	0·31	Value for polychaetes taken
IX	Unidentified material	0·14	Jones (1974)

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13 89 239 270 185 74   27   14 fish
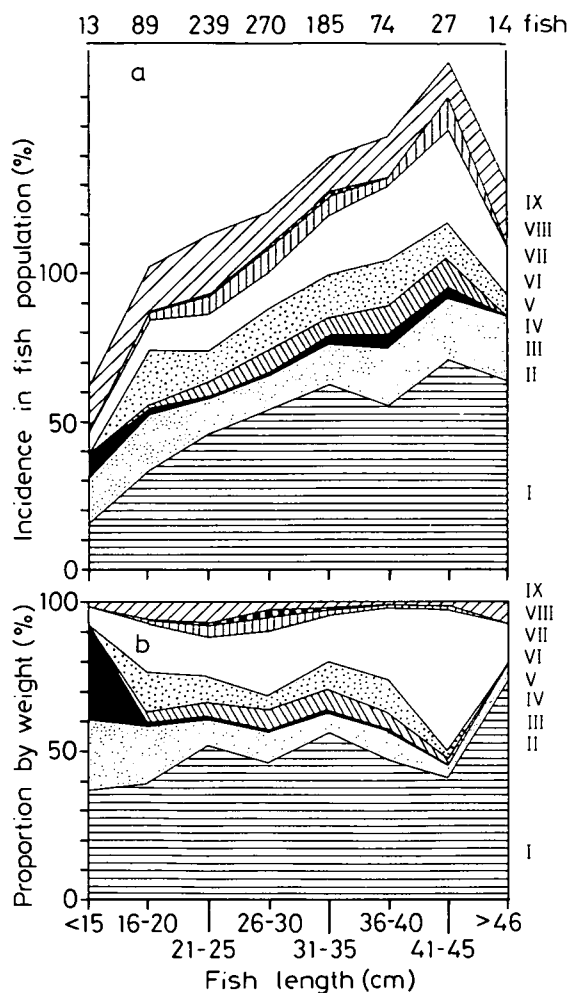
Figure 13. Composition of the food found in the stomachs of cod of differing lengths at Loch Torridon. The different categories of food are defined in Table 12. (a) Incidence of occurrence of different food items, as a percentage of the fish sampled which contain each given food item. (b) Proportion by weight of different food items.

as in Table 12. The incidence of occurrence of the various categories of food (defined as the percentage of the population containing food of that category) in fish of differing length, and their proportion by weight, are shown in Figure 13. Large epibenthic crustaceans (I) dominated the diet of fish of all sizes. The proportion of these items by weight remained high, at about half the total weight, throughout the length range, while the incidence of their occurrence within the population increased with fish length. Smaller crustaceans (II) were less important, and though their incidence remained about the same their proportion by weight declined in larger fish. Gastropods (III) were never very important in incidence or proportion by weight, and the very high proportion found in fish of the smallest length range was biased by a large quantity of material found in a single

stomach. Bivalve molluscs (IV), and polychaete worms (V) were evidently of interest to fish over a wide length range, though their total contribution to the stomach contents was relatively small. Fish (VI) increased in both incidence and proportion by weight as the cod grew larger, except for the very largest size category (where the sample size was small), and clearly contributed very significantly to the diet. Other items, like echinoderms (VII), nemertines and priapulids (VIII) appeared to be relatively unimportant, though they were taken by fish of a wide length range. Only a small part of the diet consisted of unidentified material (IX).

The mean weight of food in the stomachs increased greatly with fish length (Fig. 14), except for the very largest fish, where the weight showed a decline (though only 14 fish were sampled for this length category). There was a clear trend for the mean weight of the individual prey items in the stomachs to increase with fish length, while the mean numbers of items in the stomach showed an upward trend with length for the smaller fish, but levelled off for fish above 26 cm and then declined. Thus, the increased quantity of food in the stomachs of larger fish essentially reflected the larger size of
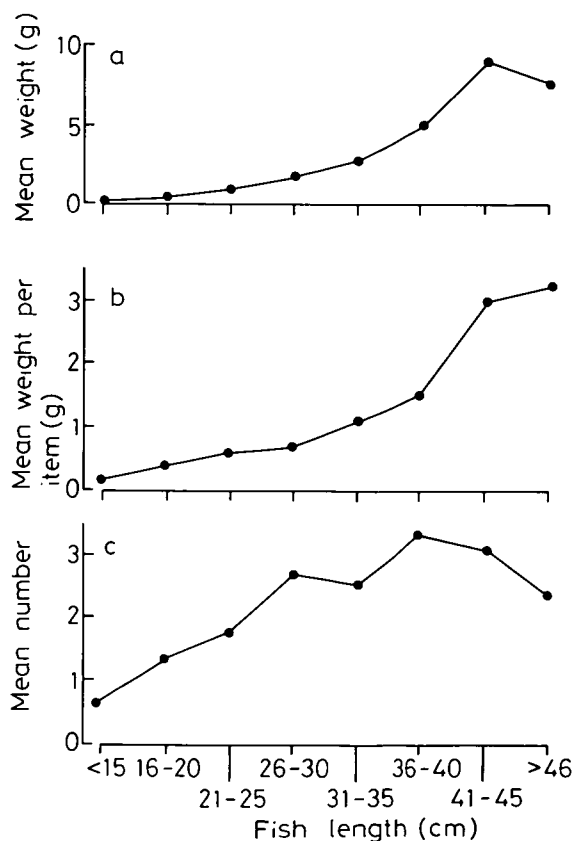

Figure 14. The quantities of food found in the stomachs of cod of differing lengths at Loch Torridon. (a) Mean weight of food. (b) Mean weight of the individual food items. (c) Mean number of food items.

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the individual prey items. This observation was confirmed for the major food items, including hermit crabs (where the mean length of great chelae found in the stomachs also increased with fish length).

Changes in diet with time of year

Seasonal changes in the incidence of different items in cod stomachs, and the proportion of these items by weight at different times of the year are shown in Figure 15. The data plotted were means taken from fish of all lengths. Data were also extracted for fish of a restricted length range (26 to 40 cm), but showed no major differences. The larger decapod crustacea (I) occurred in a higher proportion of fish, and assumed a greater proportion of weight throughout the summer and autumn, reaching minima in the winter, when the smaller crustaceans (II) increased in both incidence and proportion by weight. Fish (VI) occurred in a higher proportion of the cod, with a higher mean weight, in May/June. Nemertines and priapulids appeared mainly in the second half of the year.

The mean weight of all food in the stomachs was highest in May/June and lowest in January/February
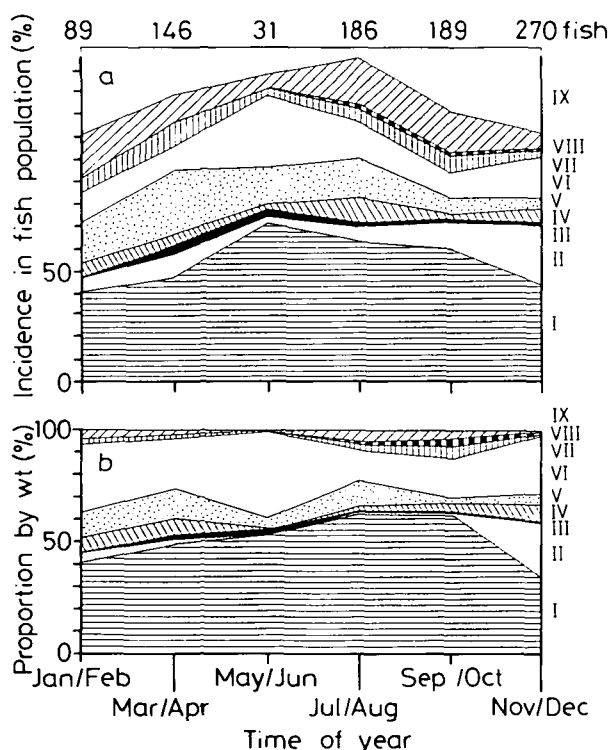

Figure 15. Composition of the food found in the stomachs of cod at Loch Torridon at different times of the year. The different categories of food are defined in Table 12. (a) Incidence of different food items, as a percentage of the fish sampled. (b) Proportion by weight of different food items.
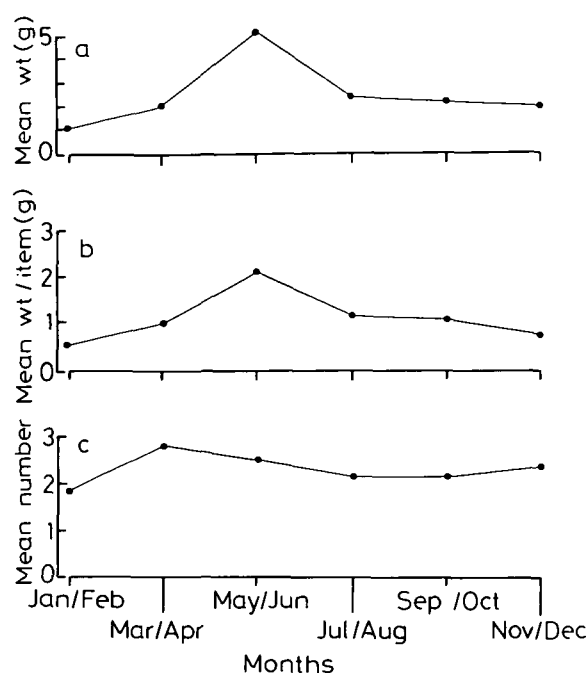

Figure 16. The quantities of food found in the stomachs of cod at Loch Torridon at different times of the year. (a) Mean weight of food. (b) Mean weight of the individual food items. (c) Mean number of food items.

(Fig. 16). Generally, the cod contained approximately the same number of prey throughout the year. In May/June, when they were most full, they contained larger prey items.

Estimation of food intake

The mean weights of food items in fish stomachs are only poor indicators of their relative contribution to food intake. Several workers have emphasized the importance of food quality, and in particular the ease with which the food material can be broken down and assimilated (Windell, 1967; Elliott, 1972; Jones, 1974; Tseitlin, 1980; MacDonald, Waiwood and Green, 1982). Different food items are digested and eliminated from the stomach at different rates. Items which are digested slowly will persist in the stomach for longer, and the resultant high mean weight of the item in the stomach will give a false impression of its importance. In principle, these differences in digestibility can be compensated for, and the quantities of different foodstuffs consumed per unit time estimated from the stomach contents, provided that the rate of elimination or evacuation of the particular materials from the stomach is known (Bajkov, 1935; Windell, 1967; Magnuson, 1969; Jones, 1974; Elliott and Persson, 1978). The precise method to be applied has varied. Jones (1974) has described a method applicable to a predator like the cod, consum-

ing large, slowly digested items at relatively infrequent intervals, where the rate of food ingestion is calculated from the mean weights of food in the stomachs of fish sampled at random. It is assumed that the mean weight in the stomachs of a given group of fish is representative of a steady state level, and thus that the ingestion rate is equal to the rate at which food is eliminated from the stomach. Essential for the analysis is knowledge of the size of the fish, the water temperature, and an experimentally determined coefficient of elimination for the appropriate food material.

We have taken the mean stomach content weights for items of the different categories found in the stomachs of cod and have applied Jones's formula. Thus, the rate at which food entered the stomach was assumed to be equal to the rate of elimination (r, grams per hour), which was determined from Jones's equation.

$$r = (Q\ L^{1\cdot4}W^{0\cdot5}10^{0\cdot035(T-12)})/175\ g\ h^{-1}$$

where L is the fish length in cm, W is the mean weight of fresh food in g in the stomachs of the fish (obtained by multiplying the formalin-preserved weights by an experimentally determined factor of 1·033), and T is the temperature (°C). Coefficients of elimination (Q, g h⁻¹) for the different food items were either taken from Jones (1974), determined experimentally, or estimated from data on similar items. Table 12 gives the values for Q for a standard fish length of 40 cm at a standard temperature of 12°C. The equation above corrects the results for the observed length of fish at the appropriate sea temperature.

In Figure 17 we have plotted the estimated total food intake for cod of differing length, averaged over the year, broken down into different food categories. The data confirm that there is a steep increase in food intake with increase in length, though the largest fish show a decline (perhaps influenced by the small sample size).
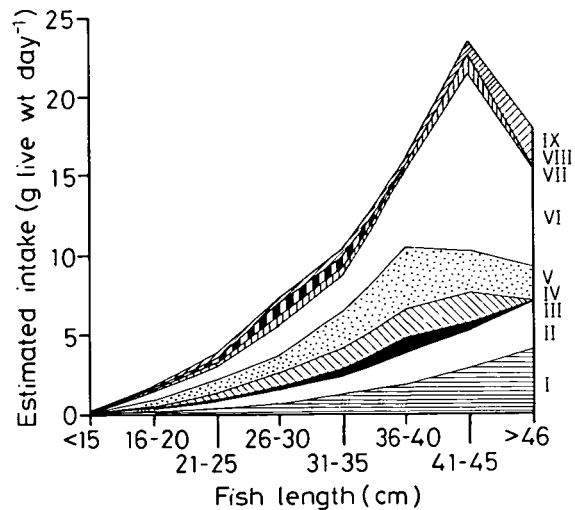

Figure 17. Estimated daily food intake (grams live weight per day) of cod of differing lengths at Loch Torridon, averaged over the year. The data are derived from stomach content analyses. The intake is broken down into different categories of food (defined in Table 12).

Especially notable is the great importance of fish in the diet. Larger crustaceans are less important than their occurrence in the stomachs would suggest, reflecting their lower rate of elimination.

Figure 18 shows change in the rate of food intake at different times of the year, averaged for fish of all lengths. It reveals that the fish are feeding most actively in the summer and autumn, rather later than is indicated by the volume of food in the stomachs (Fig. 16).

To confirm the validity of these calculations we have estimated the food intake of fish of differing age (in quarter years), applying appropriate seasonal temperature corrections, and have compared the resultant val-
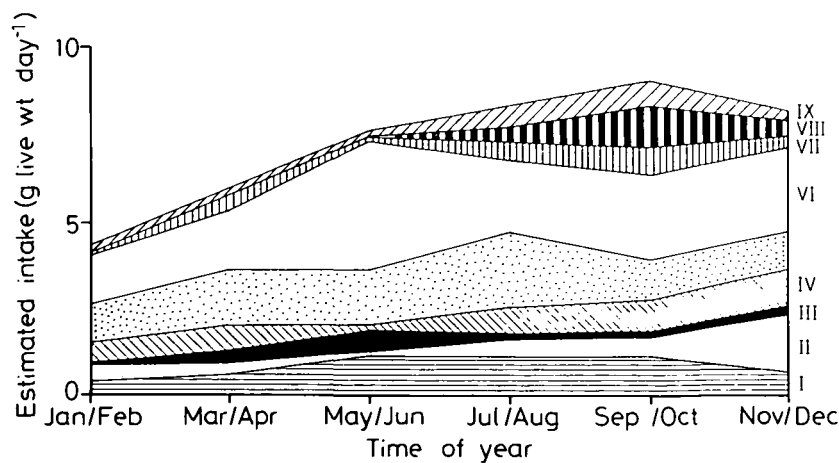

Figure 18. Estimated daily food intake (grams live weight per day) of cod at Loch Torridon at different times of the year. The data are derived from stomach content analyses. The intake is broken down into different categories of food (defined in Table 12).

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Table 13. Estimated daily intake of food items of differing categories consumed by juvenile cod (grams live weight per day), calculated from the mean weights of these food items in the stomachs of fish of differing age, adjusted for seasonal changes in temperature. The mean length of the cod, in cm, and the mean quarter-year sea temperature in °C, are also given. The different food categories are defined in Table 12.

Age (quarter years):	Q_2	Q_3	Q_4	Q_5	Q_6	Q_7	Q_8	Q_9	Q_{10}	Q_{11}	Q_{12}	Q_{13}	Q_{14}	Q_{15}
Equivalent months:	JJA	SON	DJF	MAM	JJA	SON	DJF	MAM	JJA	SON	DJF	MAM	JJA	SON
Temp. (°C):	11·14	11·69	7·86	7·11	11·14	11·69	7·86	7·11	11·14	11·69	7·86	7·11	11·14	11·69
Mean fish length (cm):	8·5	14·8	19·1	19·1	23·6	26·3	29·0	30·0	33·3	35·6	35·3	40·1	43·9	48·3
Food categories														
I	0·018	0·179	0·118	0·183	0·667	0·785	0·762	1·053	1·842	1·595	1·427	2·622	5·590	4·249
II	0·000	0·198	0·259	0·283	0·472	1·454	0·389	0·000	0·570	3·597	0·000	0·000	2·027	1·231
III	0·145	0·000	0·268	0·141	0·068	0·260	0·294	0·627	0·290	0·417	0·000	0·000	0·000	0·000
IV	0·000	0·000	0·000	0·000	0·614	1·108	0·970	0·184	1·358	1·496	0·000	1·351	0·000	0·000
V	0·000	0·000	0·619	0·444	0·819	0·856	1·857	1·572	3·762	3·178	2·986	0·000	0·000	6·096
VI	0·000	0·159	0·288	0·473	1·684	1·904	2·180	2·515	1·790	5·881	2·986	10·430	0·000	11·834
VII	0·000	0·000	0·228	0·000	0·291	0·276	0·371	0·199	1·006	0·589	1·092	0·000	0·000	4·795
VIII	0·000	0·000	0·000	0·000	0·535	0·180	0·000	0·000	0·720	1·185	0·000	0·000	0·000	0·000
IX	0·016	0·026	0·193	0·187	0·318	0·399	0·373	0·365	0·847	0·839	0·000	0·000	2·987	0·000
Total	0·179	0·561	1·973	1·710	5·468	7·223	7·197	6·515	12·103	18·777	5·505	14·402	10·603	28·207

ues (Table 13) with those obtained by calculation from the growth rates of fish in the wild (Table 10).

Figure 19 shows the changes in the total daily food intake of fish of differing age, estimated by the two alternative methods. The proportion of the daily rations devoted to maintenance, derived from growth experiments, has also been included. Both sets of data on the daily food intake are broadly similar. They show a great increase in food intake as the fish grow older. Moreover, both sets of data show that there is a strong decline in food intake during winter/spring. The decline is especially apparent at the end of the third year of life (Q_{12}), where it occurs rather earlier than in the previous two years. This early occurrence of the winter decline in large fish almost certainly biases the results presented in Figure 18 towards an earlier part of the year. It should
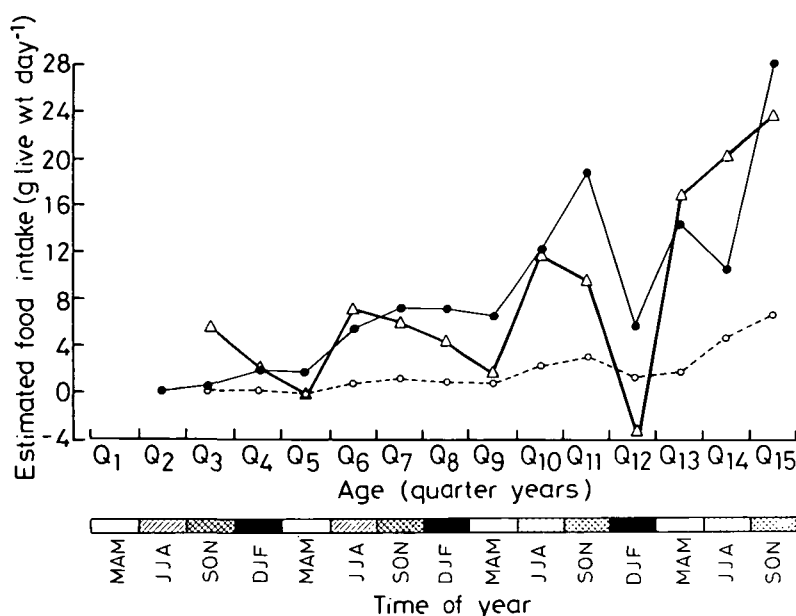

Figure 19. Estimated daily food intake (grams live weight per day) consumed by juvenile cod of differing age in Loch Torridon, derived by two independent methods. The heavy line (with triangles) shows the total food intake, and the broken line (with open circles) shows the maintenance ration, derived from growth/ration data (Table 10). The lighter line (with solid circles) shows the total food intake derived from stomach content analyses (Table 13).

also be noted that the winter decline is not so apparent from the stomach data as it is from the growth data, perhaps because our fishing method may have selected actively feeding fish for stomach sampling, at a time when the majority may not have been feeding. The food intake estimated from the stomach contents is also generally higher than that calculated from the growth rate except for the younger fish, a discrepancy which may result from the latter being an underestimate, for the several reasons discussed previously. However, the estimate derived from stomach contents analysis is dependent upon the values taken for the coefficient of elimination, Q. We have taken the best values available, but further experiments might indicate that these values are inappropriate. The value taken for fish material (category VI) is particularly open to question since it was obtained for fish fillets. Whole fish might be expected to have a lower Q, resulting in a decrease in the estimate of food intake.

Discussion

The behaviour of cod in Loch Torridon

Cod spawn off the coasts of Scotland in the spring (West, 1970). Initially, the pelagic eggs and larvae undergo a phase of dispersal in the surface waters, but by August the post-larval fish have largely disappeared from midwater catches, and have settled on the seabed to begin a phase of benthic existence. Our tagging studies and fishing observations in Loch Torridon show that many juvenile cod settle in the loch at an age of 4 to 7 months, and that they may remain there until they are between 2 and 4 years old (Fig. 3).

Acoustic tracking observations on the larger fish (over 30 cm) in the summer and autumn show that the fish live near the seabed around the edge of the loch at depths of between 10 and 20 m, moving within restricted home ranges (Hawkins *et al.*, 1980). The majority of cod exhibit a diurnal pattern of activity, but several have proved to be nocturnal. The levels of swimming activity shown by the fish are remarkably low; the mean swimming speed is less than 0·1 body length per second. From laboratory observations on the energetic costs of swimming at different speeds (Soofiani and Priede, 1983) it has been estimated that the contribution of swimming to the total energy budget of the fish in summer is less than 2 %. However, this estimate does not take account of brief bouts of activity, such as those involved in prey capture and escape from predators, which may well be particularly expensive in terms of the energy consumed. Nevertheless, in general the juvenile cod is not a highly active species. Measurements of the oxygen consumption of feeding cod (Soofiani and Hawkins, 1982) show that the metabolic costs of food processing are high: the oxygen consumption of well-fed fish is close to the maximum sustainable rate, leaving little metabolic scope for activity.

Estimates of the densities of juvenile cod within Inner Loch Torridon have been made by the tag/recapture method (the Schumacher and Eschmayer technique described by Ricker, 1975). The mean density of cod in the shallower parts of the loch was estimated to be between 10 and 50 fish per hectare (Smith and Hawkins, unpublished). This figure is an underestimate, since very small fish were under-represented in the catches. From tracking studies it appears that the total area of each home range is about 1 to 1·5 hectares (Hawkins *et al.*, 1980). The home ranges of individuals must therefore show a considerable degree of overlap, unless they are defended territories exclusive to individuals, in which case there would be a large proportion of displaced fish without territories. All the fish tracked so far have remained within a home range, and it seems probable that these ranges simply represent familiar areas, to which the fish confine their search for food.

Feeding and growth

During their initial pelagic phase, young cod of up to 3 or 4 cm in length consume zooplankters, like copepods, euphausiids, appendicularians, and the larvae of fish and decapods (Robb and Hislop, 1980; Robb, 1981). Later, their diet includes amphipods, isopods, corophiids, ostracods, and polychaetes (Daan, 1973): prey organisms which are more closely associated with seaweeds and with the sea floor. In Loch Torridon, having settled to a benthic existence, the population maintains a fairly varied diet including a range of large and small crustaceans, polychaetes, and small fish, together with small quantities of gastropods, lamellibranchs, nemertines, and echinoderms. The relative proportions of the different prey organisms do not vary greatly as the fish grow larger, though the mean size of the individual food items progressively increases. The cod show great disparities in their growth rates, however, which may be linked with differing food specializations, as may be indicated by the presence of both diurnal and nocturnal individuals in the population. Different home areas may also vary in the quantities and types of food they can offer.

The food intake of the fish was estimated by two independent methods: first from the growth rate, by comparing the growth at different feeding levels in the laboratory to growth rates measured in Loch Torridon; and secondly from the stomach contents, by calculating food intake rates using Jones's (1974) formula. Although both estimates gave quite similar results there were discrepancies, the former being consistently smaller (Fig. 19). This difference may have arisen from biases in the former as already discussed. The data indicate that many of the individual cod in the loch are feeding and growing at rates well below the maximum possible, which suggests that food may be limiting.

It is well established that both the standing crop and

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production of macrobenthos tend to be high inshore, especially in areas of reduced salinity (Wolff and de Wolf, 1977; Warwick *et al.*, 1978). The 55−60 m contour often divides a rich shallow water fauna from a sparse deeper-water one (McIntyre, 1961). The shallow margins of Scottish sea lochs may well be particularly productive, making them especially suitable as nursery grounds for benthic feeding predators. Certainly surveys of the macrobenthos within these lochs have yielded quite high standing crops, of about 30 to 40 g m⁻² (McIntyre, 1961; McIntyre and Eleftheriou, 1968), much higher than those found offshore in the North Sea (about 6 g m⁻² on the rather deeper Fladen Ground). Other data from shallow-water areas show similar and often higher values (Beukema, 1974; Ziegelmeier, 1978; Wolff and de Wolf, 1977; Warwick *et al.*, 1978). Estimates of the annual production can be made by multiplying the standing crop by a production/biomass (P/B) ratio. Typical P/B ratios vary, but Rachor (1982) suggests values of between 0·7 and 2·5 for northern coastal waters. Taking a value of 1·5 for the P/B ratio in the infralittoral zone of Loch Torridon gives an estimated macrobenthic production of about 45 g m⁻² year⁻¹ live weight. This is almost certainly a conservative estimate, since it essentially includes only the benthic in-fauna. The more active epifauna are rarely sampled adequately. Much higher estimates are available for some inshore areas (for example, those of Warwick *et al.*, 1978, for Carmarthen Bay).

Estimates of the food requirements of the cod population can also only be very approximate. If we take an estimated 30 cod per hectare for Loch Torridon (0·003 fish m²) and apply a consumption rate of about 6 g day⁻¹ (2200 g yr⁻¹) for an average cod, we obtain an annual food requirement for the population of about 6.6 g m⁻² yr⁻¹. This approximate figure suggests that the annual production of macrobenthic prey is more than sufficient to meet the requirements of the cod population. However, as Warwick *et al.* (1978) have stressed, the total macrofaunal production is not necessarily all available for fish to consume. They suggest that less than half the total production is available for export from the macrobenthic community. This output must be shared between several species of predator, which in Loch Torridon include adult flatfish, for example dabs (*Limanda limanda*) and juvenile saithe (*Pollachius virens*), lythe (*P. pollachius*), and whiting (*Merlangius merlangus*) as well as a variety of large crustaceans. Moreover, though the annual production and standing crop of food organisms may be high, from the standpoint of the individual fish it is the actual numbers of prey which are vulnerable to attack at any given time which are important.

Aquarium observations show that many of the larger prey organisms consumed by cod are difficult to capture. The home range behaviour shown by the larger fish, together with the low level of movement from place to place, suggests that the cod may spend a great deal of time stalking and then attacking their prey. Though the home ranges of different individual fish may

overlap, it is possible that there is competition between cod for particular areas of prey concentration, and that this might account for the disparities between the growth rates of individual fish.

Seasonal changes in growth and feeding

During the winter, as temperature drops, there is an increase in the proportion of cod showing a hyaline zone of reduced growth at the outer edge of the otolith. The catch per unit effort declines to a minimum, and the stomach content data show that this period is one of reduced feeding. Growth rates fall, and the condition factor of the fish rapidly declines (Fig. 1). If fish are maintained at low temperatures in the laboratory during the winter, however, they continue to feed. Indeed, their maintenance requirements are lower than in summer and they show an increased gross conversion efficiency (Figs. 9 and 10).

We must therefore conclude that the low growth rate and poor condition factors we have observed in wild fish in winter largely result from a reduction in the numbers of vulnerable prey present. Few of the prey organisms consumed by cod are annual, but some of them make offshore migrations (for example, the hermit crab (*Pagurus bernhardus*); Pike and Williamson, 1959), while others may be much less active or bury themselves in the substrate. Some may experience high winter mortalities. Our own studies have shown that catch per unit effort of the larger crustaceans in baited traps (including *Pagurus, Cancer*, and *Carcinus*) declines steeply in winter. The infralittoral étage (Glemarec, 1973) is generally characterized by strong seasonal changes compared with areas farther offshore, and many species of the infralittoral macrofauna show greatly reduced abundance during the winter (Rachor and Gerlach, 1978). Though Loch Torridon is sheltered from the effects of storms, and has a more stable substrate than more open parts of the infralittoral, the winter temperatures are up to 8°C lower than summer temperatures, and this change may have severe effects upon the benthic food of the cod.

The decline in c.p.u.e. shown for cod during the winter suggests that the fish change their behaviour in response to the decline in the food supply. They are either more reluctant to accept food when it is offered as bait, or they do not encounter the bait so often – either because they are less active or because they have moved out of the area into deeper or offshore waters. A period of high activity at this time, without a corresponding increase in food intake, would impair growth and result in our underestimating food consumption. Low c.p.u.e. and therefore difficulty in catching suitable subjects has meant that we have not been able to track individuals in winter, and know little of their movements. Conventional tagging shows that some fish are found in the same area of the loch both before and after winter. If there is an offshore migration, then at least some fish

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subsequently return. It is possible that many of the larger fish leave the loch in the winter and remain offshore. The few tag returns obtained from outside the loch suggest that the adults distribute themselves widely throughout the Minch.

We conclude that the limits to the growth and production of juvenile cod are largely set during the winter through a reduction in the availability and/or vulnerability of prey. Though the annual production of epibenthic organisms may be high in Loch Torridon, prey appear to be more available and vulnerable in the summer, from May/June onwards. At this time there may be wide disparities in the growth rates of individuals, but the majority are growing and improving greatly in condition (Fig. 1). However, a markedly different state of affairs prevails during the winter, though the exact nature of the seasonal changes needs further study. It is possible that much of the energy accumulated by fish in the summer is subsequently expended in maintaining the fish throughout the winter. This winter phase may be of crucial importance in determining the carrying capacity of the loch, affecting the growth rate of individual fish and perhaps deciding the timing of recruitment to the adult population offshore.

Acknowledgements

References

Averett, R. C. 1969. Influence of temperature and material utilization by juvenile coho salmon. Ph.D. thesis, Oregon State University, Corvallis, Oregon, USA. 74 pp.

Bajkov, A. D. 1935. How to estimate the daily food consumption of fish under natural conditions. Trans. Am. Fish. Soc., 65: 288–289.

Beukema, J. J. 1974. Seasonal changes in the biomass of the macrobenthos of a tidal flat area in the Dutch Wadden Sea. Neth. J. Sea Res., 8: 94–107.

Beverton, R. J. H., and Holt, S. J. 1957. On the dynamics of exploited fish populations. Fishery Invest. Lond., Ser. 2, 19: 533 pp.

Brett, J. R. 1970. Fish – the energy cost of living. In Marine aquaculture, pp. 37–52. Ed. by W. J. McNeil. Oregon State University Press, Corvallis, Oregon, USA. 172 pp.

Brett, J. R., Shelbourn, J. E., and Shoop, C. T. 1969. Growth rate and body composition of fingerling sockeye salmon, Oncorhynchus nerka, in relation to temperature and ration size. J. Fish. Res. Bd Can., 26: 2363–2394.

Brown, M. E. 1957. Experimental studies on growth. In The physiology of fishes, vol. 1, pp. 361–400. Ed. by M. E. Brown. Academic Press, New York, 447 pp.

Condrey, R. E. 1982. Ingestion-limited growth of aquatic animals: the case for Blackman Kinetics. Can. J. Fish. Aquat. Sci., 39: 1585–1595.

Daan, N. 1973. A quantitative analysis of the food intake of North Sea cod (Gadus morhua L.). Neth. J. Sea Res., 6: 479–517.

Daan, N. 1974. Growth of North Sea cod, Gadus morhua, Neth. J. Sea Res., 8: 27–48.

Davies, P. M. C., and Massey, S. M. 1977. Energy conversion efficiency in fish: The influence of food intake and temperature on K-line at rations close to maintenance. J. comp. Physiol., 144: 191–202.

Elliott, J. M. 1972. Rates of gastric evacuation in brown trout, Salmo trutta L. Freshwat. Biol., 2: 1–18.

Elliott, J. M., and Persson, L. 1978. The estimation of daily rates of food consumption for fish. J. Anim. Ecol., 47: 977–993.

Glemarec, C. M. 1973. The benthic communities of the European North Atlantic continental shelf. Oceanogr. mar. Biol., Ann. Rev., 11: 263–289.

Hawkins, A. D., Urquhart, G. G., and Smith, G. W. 1980. Ultrasonic tracking of juvenile cod by means of a large spaced hydrophone array. In A handbook of biotelemetry and radio tracking, pp. 461–470. Ed. by C. J. Amlaner Jr., and D. W. MacDonald. Pergamon Press, Oxford. 804 pp.

Ivlev, V. S. 1945. The biological productivity of waters. Usp. Sovrem. Biol., 19: 98–120. (Engl. transl., J. Fish. Res. Bd Can., 23: 1727–1759 (1966)).

Jensen, A. C. 1967. Effects of tagging on the growth of cod. Trans. Am. Fish. Soc., 96: 37–41.

Jobling, M. 1983. Growth studies with fish – overcoming the problems of size variation. J. Fish. Biol., 22: 153–157.

Jones, R. 1974. The rate of elimination of food from the stomachs of haddock Melanogrammus aeglefinus, cod Gadus morhua, and whiting Merlangius merlangus. J. Cons. int. Explor. Mer, 35: 225–243.

Jones, R., and Hislop, J. R. G. 1978. Further observations on the relation between food intake and growth of gadoids in captivity. J. Cons. int. Explor. Mer, 38: 244–251.

Kelso, J. R. M. 1972. Conversion, maintenance, and assimilation for walleye, Stizostedion vitreum vitreum, as affected by size, diet, and temperature. J. Fish. Res. Bd Can., 29: 1181–1192.

Kohler, A. C. 1963. Variations in the growth of Atlantic cod (Gadus morhua L.). J. Fish. Res. Bd Can., 21: 57–100.

Law, E. A., and Archie, J. W. 1981. Appropriate use of regression analysis in marine biology. Mar. Biol., 65: 13–16.

Love, R. M. 1980. The chemical biology of fishes. Academic Press, London. 943 pp.

MacDonald, J. S., Waiwood, K. G., and Green, R. H. 1982. Rates of digestion of different prey in Atlantic cod (Gadus morhua), ocean pout (Macrozoarces americanus), winter flounder (Pseudopleuronectes americanus), and American plaice (Hippoglossoides platessoides). Can. J. Fish. Aquat. Sci., 39: 651–659.

McIntyre, A. D. 1961. Quantitative differences in the fauna of boreal mud associations. J. mar. biol. Ass. U.K., 41: 599–616.

McIntyre, A. D., and Eleftheriou, A. 1968. The bottom fauna of a flatfish nursery ground. J. mar. biol. Ass. U.K., 48: 113–142.

Magnuson, J. J. 1969. Digestion and food consumption by skipjack tuna, Katsuwonus pelamis. Trans. Am. Fish. Soc., 98: 379–392.

Marsh, J. B., and Weinstein, D. B. 1966. Simple charring method for determination of lipids. J. Lipid Res., 7: 574–576.

Niimi, A. J., and Beamish, F. W. H. 1974. Bioenergetics and growth of largemouth bass (Micropterus salmoides) in relation to body weight and temperature. Can. J. Zool., 52: 447–456.

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Paloheimo, J. E., and Dickie, L. M. 1966. Food and growth of fishes. II. Effect of food and temperature on the relation between metabolism and body weight. J. Fish. Res. Bd Can. 23: 869–908.

Pandian, T. J. 1970. Intake and conversion of food in the fish *Limanda limanda* exposed to different temperatures. Mar. Biol., 5: 1–17.

Phillipson, J. 1964. A miniature bomb calorimeter for small biological samples. Oikos, 15: 130–139.

Pike, R. B., and Williamson, D. I. 1959. Observations on the distribution and breeding of British hermit crabs and the stone crab. Proc. Zool. Soc. London., 132: 551–567.

Rachor, E. 1982. Biomass distribution and production estimates of macroendofauna in the North Sea. ICES CM 1982/L:2, 10 pp. (mimeo).

Rachor, E., and Gerlach, S. A. 1978. Changes of macrobenthos in a sublittoral sand area of the German Bight, 1967 to 1975. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 172: 418–431.

Ricker, W. E. 1973. Linear regressions in fishery research. J. Fish. Res. Bd Can., 30: 130–139.

Ricker, W. E. 1975. Computation and interpretation of biological strategies of fish populations. Bull. fish. Res. Bd Can., 191: 382 pp.

Robb, A. P. 1981. Observations on the food and diel feeding behaviour of pelagic 0-group gadoids in the northern North Sea. J. Fish. Biol., 18: 183–194.

Robb, A. P., and Hislop, J. R. G. 1980. The food of five gadoid species during the pelagic 0-group phase in the northern North Sea. J. Fish. Biol., 16: 199–217.

Soofiani, N. M., and Hawkins, A. D. 1982. Energetic costs at different levels of feeding in juvenile cod *Gadus morhua* L. J. Fish. Biol., 21: 577–592.

Soofiani, N. M., and Priede, I. G. 1985. Aerobic metabolic scope and swimming performance in juvenile cod, *Gadus morhua* L. J. Fish. Biol. (In press).

Strickland, J. D. H., and Parsons, T. R. 1972. A practical handbook of sea water analysis. Bull. Fish. Res. Bd Can., 167: 310 pp.

Trout, G. C. 1957. The Bear Island cod, migrations and movements. Fishery Invest. Lond., Ser. 2, 7: 51 pp.

Tseitlin, V. B. 1980. Duration of gastric digestion in fishes. Mar. Ecol. Prog., Ser., 2: 277–280.

Warwick, R. M., George, C. L., and Davies, J. R. 1978. Macrofaunal production in a *Venus* community. Estuarine Coastal Mar. Sci., 7: 215–241.

West, W. Q.-B. 1970. The spawning biology and fecundity of cod in Scottish waters. Ph.D. thesis, Aberdeen University, Aberdeen, Scotland. 257 pp.

Windell, J. T. 1967. Rates of digestion in fishes. *In* Biological basis of freshwater fish production, pp. 151–173. Ed. by S. D. Gerking. Blackwell, Oxford. 495 pp.

Wolff, W. J., and de Wolf, L. 1977. Biomass and production of zoobenthos in the Grevelingen Estuary, The Netherlands. Estuarine Coastal Mar. Sci., 5: 1–24.

Ziegelmeier, E. 1978. Macrobenthos investigations in the eastern part of the German Bight from 1950 to 1974. Rapp. P.-v. Réun. Cons. int. Explor. Mer, 172: 432–444.