Netherlands Journal of Sea Research
34 (1-3): 139-147 (1995)

GROWTH OF JUVENILE HALIBUT (*HIPPOGLOSSUS HIPPOGLOSSUS*) RELATED TO TEMPERATURE, DAY LENGTH AND FEEDING REGIME

HOGNE HALLARÅKER, ARILD FOLKVORD* and SIGURD O. STEFANSSON

Department of Fisheries and Marine Biology, University of Bergen, Bergen High Technology Center, N-5020 Bergen, Norway

ABSTRACT

Experimental studies with farmed juvenile halibut, *Hippoglossus hippoglossus*, were undertaken to optimize rearing procedures. Extended feeding period and/or day length did not significantly increase growth rates of juvenile halibut of 5 to 20 g wet weight. Growth was strongly affected by temperature, and highest growth rates were obtained at 13°C followed by 10, 16 and 7°C for juveniles of 20 to 90 g. Growth rate declined with size in one of two experiments in this size interval. Q_{10} of daily growth rate between 7 and 10°C varied from 2.5 to 3.0. Individual growth always varied highly within the temperature treatments (overall range -0.3 - 3.5%·d^{-1}), but significant size rank correlations were maintained during the 12-week experiment. Juvenile halibut grew approximately isometrically from 20 to 90 g. Weight-specific oxygen consumptions of 80 g juveniles averaged 140 and 200 mg O_2 (kg·h)$^{-1}$ at 10 and 16°C, respectively, and this is comparable to rates measured for other flatfish species.

Key words: growth, halibut, juvenile, temperature, oxygen consumption, *Hippoglossus*, light, size rank

1. INTRODUCTION

Atlantic halibut (*Hippoglossus hippoglossus* L.) is the largest of the flatfish species in the North Atlantic, reaching up to 300 cm in length and 250 kg (Pethon, 1985). Declining natural stocks combined with increasing interest in cultivating the species have led to substantial research efforts on its earliest life stages. Very little is known, however, about its natural history during the larval and juvenile stages. To date a handful of larval and 0-group halibut have been collected in Norwegian waters (Haug *et al.*, 1989; Bergstad & Gordon, 1993). Young halibut have been encountered at depths of 20 to 60 m off Iceland (Sigurdsson, 1956), and based on their spotted pigmentation pattern it is assumed that the juveniles are associated with gravel and hard-bottom substrates. The temperature regime off northern Norway at these depths varies from 2.5 to 8°C.

In a study on temperature and size-dependent growth of halibut, Björnsson (1993) found higher average growth rates at 13°C than at 7 and 10°C for juvenile halibut smaller than 100 g (approx. 18 cm). A temperature optimum could not be defined at this stage, because the juveniles were not reared at higher temperatures. Subsequent experiments on juveniles with average weights larger than 140 g revealed an optimal rearing temperature for growth of around 11.4°C (Björnsson, 1993). The highest average growth rates obtained of larger fish were substantially lower, however, than at smaller sizes, 0.6%·d^{-1} at 280 g compared to 2.1%·d^{-1} at 28 g. The effect of day length on growth in these experiments was difficult to assess since the light regime during the experiments was not specified.

The present experiments were carried out to investigate whether day length affects growth rates in juvenile halibut. Additional experiments were undertaken to assess the importance of size and temperature on growth of individual juvenile halibut smaller than 100g. In these experiments temperatures up to 16°C were used to obtain growth estimates at temperatures beyond the expected optimum for growth. Further, specific oxygen consumption was measured at different temperatures to relate growth rates to metabolic costs at respective temperatures.

* *To whom correspondance should be addressed; e-mail: arild.folkvord@ifm.uib.no*

2. MATERIALS AND METHODS

2.1. BIOLOGICAL MATERIAL

Two size groups of juvenile halibut of mixed parental background were used in these experiments. The juveniles were produced extensively in plastic bags according to the methodology of Øiestad & Berg (1989) by Stolt Sea Farm Aga, western Norway. Before transfer to the experimental facility the fish were weaned to commercial formulated feed (Ewos flatfish feed, TT10), and kept outdoors under a natural photoperiod regime at water temperatures ranging from 7 to 9°C. Upon arrival at the experimental facility in Bergen High Technology Center, the two groups of juveniles were transferred to separate tanks and kept for two weeks at 10°C under natural photoperiod regime.

2.2. EXPERIMENTAL DESIGN

On 11 December 1991, 445 juveniles from the smallest size group were randomly allocated to 6 tanks and kept 34 days at ambient water temperature before the start of Experiment 1 (Exp. 1, Table 1). Three light and feeding regimes were then established; NL/NF:natural photoperiod and feeding during natural day length, 24L/NF: 24 hours of light and feeding during natural day length, 24L/24F: 24 hours of light and continuous feeding. All treatments were replicated. Another four groups of 41 to 42 fish were generated by randomly allocating fish from the largest size group. These groups were then transferred to 7, 10, 13 and 16°C at the onset of Experiment 2 (Exp. 2, Table 2). After the completion of Experiment 1, 168 juveniles from the NL/NF and 24L/NF treatments were used in a pseudoreplication of Experiment 2 using the same temperature treatments as above (Exp. 2b, Table 2). Average start weights of the juveniles were 5.8 g, 19.6 g and 20.1 g in Experiment 1, 2 and 2b, respectively.

On 6 January, all the fish in Experiment 2 were individually tagged with Fisheagle® PIT tags (Prentice *et al.*, 1986). No fish died during tagging, but three missing/malfunctioning tags were replaced after the following weighing. In Experiment 2b, 26 to 29 fish in each treatment were tagged at the start of the experiment (16 March 1992). These fish originated from the NL/NF group in Experiment 1. The remaining untagged fish in the tanks were taken from the 24L/NF group. These fish were added to obtain the same density of fish as in Experiment 2. Two tags were lost/malfunctioned during the experiment.

2.3. EXPERIMENTAL CONDITIONS

All experiments were carried out in 1 m^2 covered 500 dm^3 fibreglass tanks. The tanks were supplied with aerated water originating from 100 m depth. The water inflow in each tank was provided by a vertical perforated tube. Water flow was maintained at 15 $dm^3 \cdot s^{-1}$ throughout the experiment except during the diurnal oxygen measurements. Water outflow was through a flat circular sieve in the bottom centre of the tank, and the water height was maintained at approx. 50 cm. We used Osram L 36W/12 Lumilux de lux as light source, and the intensity and day length of these tubes were automatically controlled by a computer programme 'Lysstyr' (Hansen, 1990). Day length increased from 7 to 12 hours during Experiments 1 and 2, and from 12 to 18 hours in Experiment 2b. The light intensity at noon was set at 20% of maximum capacity of the tubes in the natural photoperiod groups, and 20% throughout in the 24L groups. Maximum light intensity measured 5 cm above the bottom of the tank varied between 50 and 150 lux during the experiments, *i.e.*, within the range documented not to influence growth in halibut (Aune *et al.*, 1994) or Atlantic salmon (Stefansson *et al.*, 1993).

In Experiments 2 and 2b temperature was measured daily and kept constant at 7, 10, 13 and 16°C (SD = 0.2). The temperature in Experiment 1 averaged 8.3°C, and declined gradually from 9.0 to 8.5°C during acclimation, and from 8.5 to 8.0°C during the experiment. The salinity remained constant at S=34.5 ±0.5 throughout all the experiments. Oxygen saturation was measured weekly in the effluent water of all tanks and was always above 86%. The fish were

TABLE 1

Experimental setup in day length/feeding regime experiment (Exp. 1). Trailing numbers in Exp. 1 treatments indicate replicate number. Different letters after mean start and final weights represent significant differences ($p < 0.05$) between groups in respective periods.

experiment	*treatment*	*n start*	*mean start weight (g)*	*SD (g)*	*n end*	*survival (%)*	*mean final weight (g)*	*SD (g)*
Exp. 1 (56 days)	NL/NF1	67	6.1 ab	2.2	66	99	18.2 a	6.2
Jan. 14 - Mar. 10	NL/NF2	71	5.5 b	2.4	70	99	17.0 a	6.4
	24L/NF1	73	6.8 a	2.2	71	97	19.0 a	5.8
	24L/NF2	74	5.2 b	2.4	70	95	16.8 a	6.3
	24L/24F1	74	5.8 ab	2.3	72	97	18.6 a	6.2
	24L/24F2	74	5.5 b	2.3	69	93	18.9 a	6.7

attended once or twice daily, and these inspections included supply of feed, removal of bottom water (10%) and monitoring of behaviour and mortality.

The fish in Experiment 1 were fed every 6 min during the feeding period, and the feed was 1.8 mm marine fish pellets produced by Felleskjøpet A/S, Bergen, Norway. In Experiments 2 and 2b we initially used 3.5 mm turbot feed pellets produced by T. Skretting A/S, Stavanger, Norway. Later on 5 mm pellets were given in proportion to the biomass of juveniles larger than 50 g. All groups were fed in excess (5% of their biomass per day) and the amounts fed were adjusted after each weighing based on previous growth rates. The 24L/24F treatment in Experiment 1 was fed 10%·d^{-1} to ensure that feed was offered at a rate similar to that of the other treatments.

2.4. DATA ANALYSIS

All the fish were individually weighed to the nearest 0.1 g wet weight every 14 days between 08h00 and 12h00 (first interval in Experiment 2 was 12 days). Standard length (SL) was measured to nearest mm. Daily growth rates were calculated as:

$$DGR = 100 \cdot (e^{g} - 1)$$

where $g = (\ln(W_2) - \ln(W_1)) / (t_2 - t_1)$ and W is wet weight (g) at respective time period (days). In the calculation of size specific growth rate, DGR was regressed against geometric mean (GM) weight in the time interval:

$$GM = (W_1 \cdot W_2)^{1/2}$$

The growth rates during acclimation (first two weeks) or during the period after tagging were not included in this analysis. One malformed specimen in the T7 treatment was also excluded in the analysis. In the calculation of the temperature effect on growth rate, Q_{10} of growth was calculated according to (Schmidt-Nielsen 1990):

$$Q_{10} = (DGR_2/DGR_1)^{10/(t_2-t_1)}$$

Log length - log weight regression were calculated in the length interval of 11 to 16.4 cm, corresponding to approx. 20 to 80 g.

Oxygen consumption measurements were carried out between 8 and 9 March (Exp. 2), and between 7 and 8 June (Exp. 2b). Open respirometry has several limitations (Steffensen, 1989), but the waterflow in the tanks were reduced to obtain a more precise estimate of the difference between oxygen content of inflowing and outflowing water. Measurements were carried out every four hours over a 24-hour period, and the biomass of the fish in the respective tanks was measured 6 days before (Exp. 2) or the day after (Exp. 2b) the oxygen measurement series. The weight specific oxygen consumption was calculated as (Jobling, 1982):

$$V_{O_2} = (V_f * dpO_2) / B$$

where V_f is the water flow, B is the biomass and dpO_2 is the partial pressure difference between inflowing and outflowing water.

Differences in growth rates between treatments were tested with one-way ANOVA. Homogeneity of variances were tested with Hartley's F-max test (Sokal & Rohlf, 1981), and all F-max values were less than 5. Tukey's HSD-test was used as post-hoc test to see which treatments differed from each other when the weight or growth rate ANOVAs were significant. The log length-log weight regressions and the size-dependent growth rates from the various temperature treatments were tested for equal slopes with ANCOVA. Treatment effects were considered significant at p-levels less than 0.05.

TABLE 2

Experimental set-up in the temperature experiments (Exp. 2 and 2b). Different letters after mean start and final weights represent significant differences ($p < 0.05$) between groups in respective periods. Data for individually tagged fish in Exp. 2b, numbers in parenthesis represent data for the entire group (* group was accidentally killed on 29 May, ** one tag lost, *** one malformed fish excluded).

experiment	*treatment*	*n start*	*mean start weight (g)*	*SD (g)*	*n end*	*survival (%)*	*mean final weight (g)*	*SD (g)*
Exp. 2 (82 days)	T7	42	18.3 a	5.8	42	100	45.9 c	14.3
Dec. 11 - Mar. 2	T10	41	21.0 a	5.5	41	100	83.3 a	20.8
	T13	42	20.8 a	5.5	42	100	90.1 a	24.4
	T16	41	18.1 a	5.1	39	95	60.9 b ***	19.9 ***
Exp. 2b (84 days)		28 (42)	20.1 (20.1) a	6.6 (6.1)	28 (42)	100	60.4 (62.3) c	17.7 (16.0)
Mar. 16 - June 8		29 (42)	20.2 (20.1) a	6.9 (6.5)	28 (42) **	100	96.1 (96.0) a	25.7 (25.2)
		26 (42)	20.6 (20.3) a	8.3 (7.8)	26 (42) *	100 *	97.5 (102.5) *	28.4 (31.7) *
		28 (42)	19.8 (19.8) a	6.1 (6.4)	27 (42) **	100	80.4 (81.3) b	29.0 (22.1)

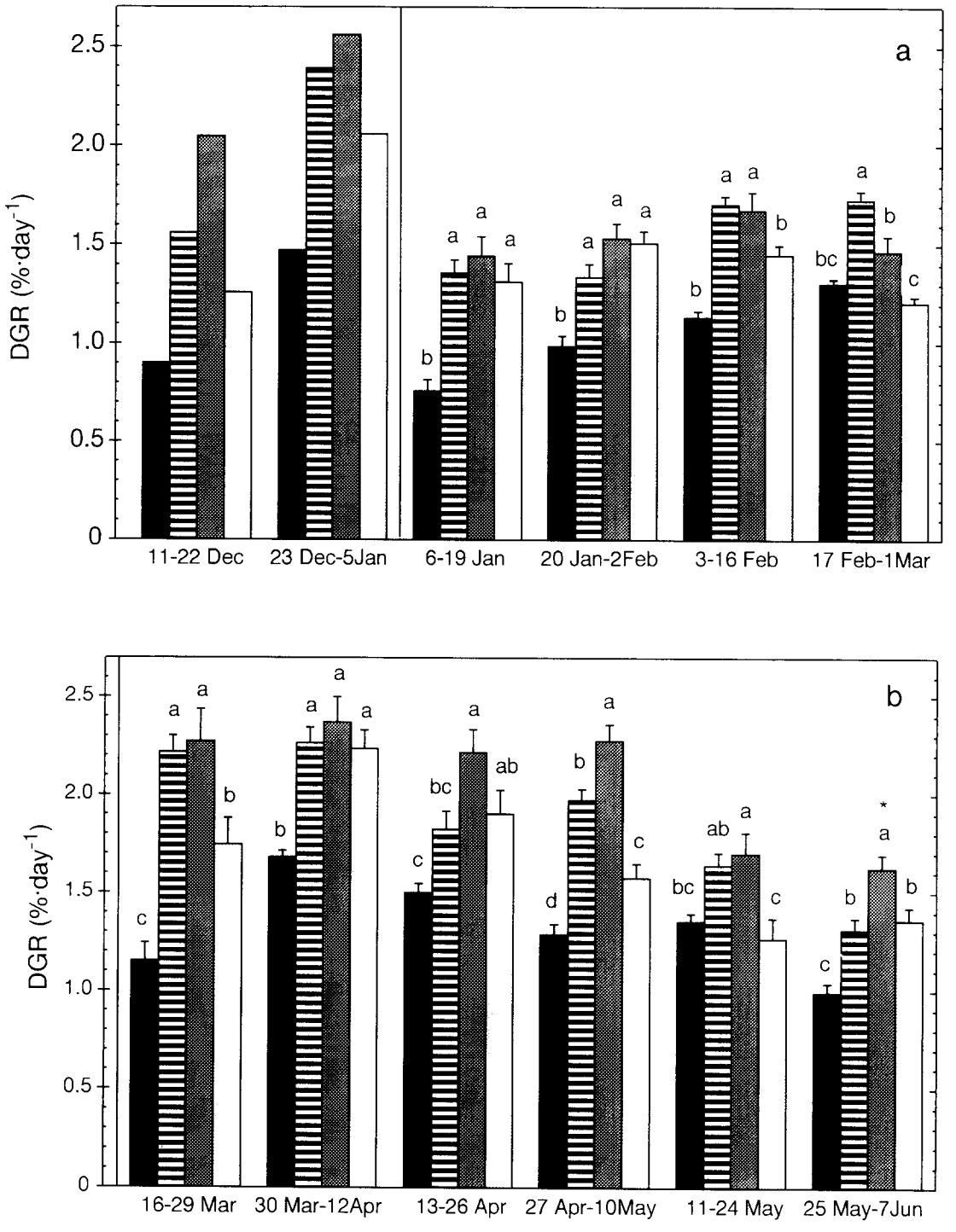

Fig. 1. Daily growth rates (DGR) during Exp. 2. Solid bar = 7°C, horizontal shading = 10°C, grey bar = 13°C and white bar = 16°C treatment. Whiskers indicate SE, and different letters represent significant differences between treatments within respective time periods with "*a*" as the highest value. Vertical line indicates time of tagging. (* The T13b group died accidentally on May 24, and DGR is calculated accordingly.)

3. RESULTS

3.1. MORTALITY

Total treatment mortality was 5% or less and did not differ between treatments. With the exception of group T13b, which was accidentally killed 10 days before the termination of the experiment, no tanks suffered more than 7% mortality during the experiments (Tables 1 and 2).

3.2. GROWTH

Mean weight in 24L/NF1 was higher than in 24L/NF2 at start, and this difference was maintained until the end of the experiment (nested ANOVA, $p < 0.05$, Table 1). Apart from this, no differences were found between treatments at any time during Experiment 1. Final weights averaged 17.5, 17.9 and 18.7 g in NL/NF, 24L/NF and 24L/24F treatments, respectively. In Experiment 2, T10 and T13 had similar mean weights throughout the experiment, and they were higher than mean weight in T16 which eventually was higher than in T7. A similar pattern was observed in Experiment 2b, but mean weight in T10b was not higher than in T16b before the end of the experiment (Table 2). In Experiments 2 and 2b, the coefficient of variation (CV) of weight was relatively constant or declined throughout the experiment in all groups.

Overall daily growth rate (DGR) in Experiment 1 averaged 2.0, 2.0 and 2.2%·d^{-1} for the NL/NF, 24L/NF and 24L/24F treatments, respectively. In Experiment 2, DGR was lower after the tagging of the juveniles (Fig. 1a). Overall growth rates in Experiment 2 averaged 1.1, 1.7, 1.8 and 1.5%·d^{-1} for the T7, T10, T13 and T16 treatments, respectively. The ranking of average DGR at the various temperatures indicated that growth was relatively higher at the lower temperatures compared to the higher temperatures towards the end of the experiment than at the start of the experiment (Fig. 1a). In Experiment 2b, the growth rate was consistently higher than in Experiment 2, even initially after the tagging of the juveniles (Fig. 1b). Overall growth rates of the individually tagged fish in Experiment 2b averaged 1.4, 1.8, 2.0 and 1.7%·d^{-1} in the T7b, T10b, T13b and T16b groups, respectively. DGR was highest at all times in the T13b group, and generally declined in all groups throughout the experiment.

The rate of change in growth rate with size was similar among treatments within experiments in Experiments 2 and 2b (Fig. 2, Table 3). The size-specific growth rate differed, however, between the two experiments. In Experiment 2, there was no change in growth rate with size (Fig. 2a, Table 3). In Experiment 2b the growth rate declined with size (Fig. 2b, Table 3). In both experiments there were significant differences between the temperature treatments (Table 3).

Q_{10} of daily growth rate was 3.0 and 2.5 between 7 and 10°C, and 0.9 and 1.5 between 10 and 13°C during Experiments 2 and 2b, respectively. Q_{10} between the various temperatures showed considerable variation in the different time periods, but tended to be higher at the beginning of the experiments.

The slopes of the log length - log weight regressions in the length range 11 to 16.4 cm were similar between treatments (ANCOVAs, $p > 0.12$). In Experiment 2 the elevation was different between treatments (ANCOVA, $p < 0.001$), but not in Experiment 2b (ANCOVA, $p = 0.053$). The magnitude of the differences in elevation was minor, however, and the common equations for the two experiments were:

$$\text{Exp. 2} \quad \ln W = -4.41 + 3.13 \cdot \ln L$$
$$\text{Exp. 2b} \quad \ln W = -4.34 + 3.09 \cdot \ln L$$

where W is wet weight in g and L is standard length in cm.

A significant size rank correlation of the tagged individuals was maintained during Experiments 2 and 2b (Spearman rank correlation, $r_s > 0.55$, $p < 0.05$). In Experiment 2 the size rank correlation declined from 0.96 in the T7 group to 0.78 in the T16 group. In Experiment 2b a similar decline with temperature was found with 0.92 in the T7b group and 0.56 in the T16b group.

The specific oxygen consumption was higher at higher temperatures in Experiments 2 and 2b (Table 4). The difference in specific oxygen consumption between 7 and 16°C was higher in Experiment 2 than in 2b.

4. DISCUSSION

Growth rate of juvenile halibut was significantly influenced by temperature and fish size. Overall growth rate was highest at 13°C (Exp. 2b) or equally high at 10 and 13°C (Exp. 2), with significant reductions in growth rate at higher (16°C) or lower (7°C) temperatures. The present results suggest that optimum temperature for growth of juvenile halibut in the size range 20 to 90 g is between 10 and 13°C, in good agreement with Björnsson (1993), who suggested 13°C and 11.4°C as optimal temperatures for growth of 26 g and 280 g halibut, respectively. In the present experiment, overall growth rates at 10 and 13°C averaged approximately 1.7% and 1.8%·d^{-1} (Exp. 2), and 1.8% and 2.0%·d^{-1} (Exp. 2b), which are higher than growth rates obtained with similar-sized juvenile halibut reported by Björnsson (1993). Little is known about distribution or temperature preferences of wild juvenile halibut in ocean waters. Scattered observations indicate that juveniles are found in waters of about 7 to 8°C in summer and 2.5 to 3.5°C in early spring (Sigurdsson, 1956), suggesting that this species is adapted to cold water conditions, with a relatively low temperature optimum for growth even at the juvenile stage. The present results document that

TABLE 3
Analysis of covariance (ANCOVA) for the regression of daily growth rate (DGR, %·d^{-1}) against geometric mean (GM) weight (W, g wet weight) at different temperatures (T, °C).

experiment	*source*	*sum of squares*	*D.F.*	*mean square*	*F-ratio*	*p*
Exp. 2	temperature (T)	10.602	3	3.534	15.57	0.000
	GM weight (W)	0.116	1	0.116	0.51	0.475
	T x W	0.808	3	0.269	1.19	0.313
	error	110.257	486	0.227		
Exp. 2b	temperature (T)	55.869	3	18.623	85.58	0.000
	GM weight (W)	38.403	1	38.403	176.477	0.000
	T x W	0.057	3	0.019	0.086	0.968
	error	118.380	544	0.218		

growth rate of juvenile halibut in culture may be enhanced by elevating water temperature to between 10 and 13°C.

Increasing temperature from 7 to 10°C gave the highest relative growth increase calculated as Q_{10} ratio of respective growth rates, while Q_{10} between 10 and 13°C was 0.9 and 1.5 in Experiments 2 and 2b, suggesting little or no positive effect of further increasing temperature for culture of juvenile halibut from 10 to 13°C. Q_{10} was less than 1.0 between 13 and 16°C, as temperature was raised above the optimum for the species. Further, specific oxygen consumption was increased by 60% from 13 to 16°C, suggesting that routine metabolism was significantly elevated at the higher temperature, partly explaining the reduction in growth rate. Also, size-dependent growth was significantly influenced by temperature. In Experiment 2, there was an inverse relation between the slopes of the size *versus* growth rate regressions and rearing temperature, with a significant positive slope in T7. In contrast, in Exp. 2b, all regressions were negative and revealed no such trend with temperature. The increase in growth rate with increasing size at lower temperatures indicates that during late winter the optimum temperature for growth was shifted downwards as the fish grew larger, in accordance with findings of Björnsson (1993) and Aune *et al.* (1994). The shift to lower optimum temperature for growth with increasing size observed in Exp. 2 further agrees with the general pattern suggested by Brett (1979). However, in late spring and early summer, growth rate decreased with increasing size at all temperatures. Under the longer day length and improved growing conditions of Experiment 2b, the overall negative correlations between fish size and growth rate are in accordance with findings on various marine fish species as well as several salmonids (see reviews by Niimi & Beamish, 1974; Brett, 1979).

Overall growth rate at all temperature regimes was higher in spring and early summer than at the same temperatures in late winter, suggesting that the increase in photoperiod during the period January-June influenced growth rate of juvenile halibut. Although not significant, a positive effect on growth was seen when juvenile halibut (size range 5 to 20 g) were exposed to continuous light between early January and early March. Following a sudden increase in day length from LD8:16 to LD24:0, a 5-10% relative increase in growth rate was seen over the next 2 months when the fish were fed throughout the 24 hour cycle, conforming to our observations from Experiments 2 and 2b. Seasonal changes in growth rate are documented in several Arctic and temperate fish species, with growth rate peaking as day length increases rapidly in late spring and early summer. Enhanced growth under naturally or artificially long or increasing day length has been clearly documented in Atlantic salmon (*Salmo salar*, Saunders *et al.*, 1985; Stefansson *et al.*, 1991; Solbakken *et al.*, 1994) and several Pacific salmonids (*Oncorhynchus* spp., Clarke *et al.*, 1978, 1981). The limited data available suggest that similar effects may be observed in juveniles of several marine fish species, *e.g.* cod (*Gadus morhua*, Folkvord & Otterå, 1993), turbot (*Scopthalmus maximus*, Imsland *et al.*, 1995), plaice (*Pleuronectes platessa*), sole (*Solea solea*, Fonds, 1979) and splitnose rockfish (*Sebastes diplopora*, Boehlert, 1981).

The present results suggest that juvenile halibut respond to photoperiod changes, although the effects are subtle when compared with those observed on salmonids. The abrupt, unnatural increase from short day length to continuous light may have been inappropriate in stimulating a growth response in juvenile

TABLE 4
Average specific oxygen consumption (mg O_2·kg·h^{-1}) of juvenile halibut in Exp. 2 and Exp. 2b.

experiment / temperature	*7°C*	*10°C*	*13°C*	*16°C*
Exp. 2	106	121	126	205
Exp. 2b	144	157		198

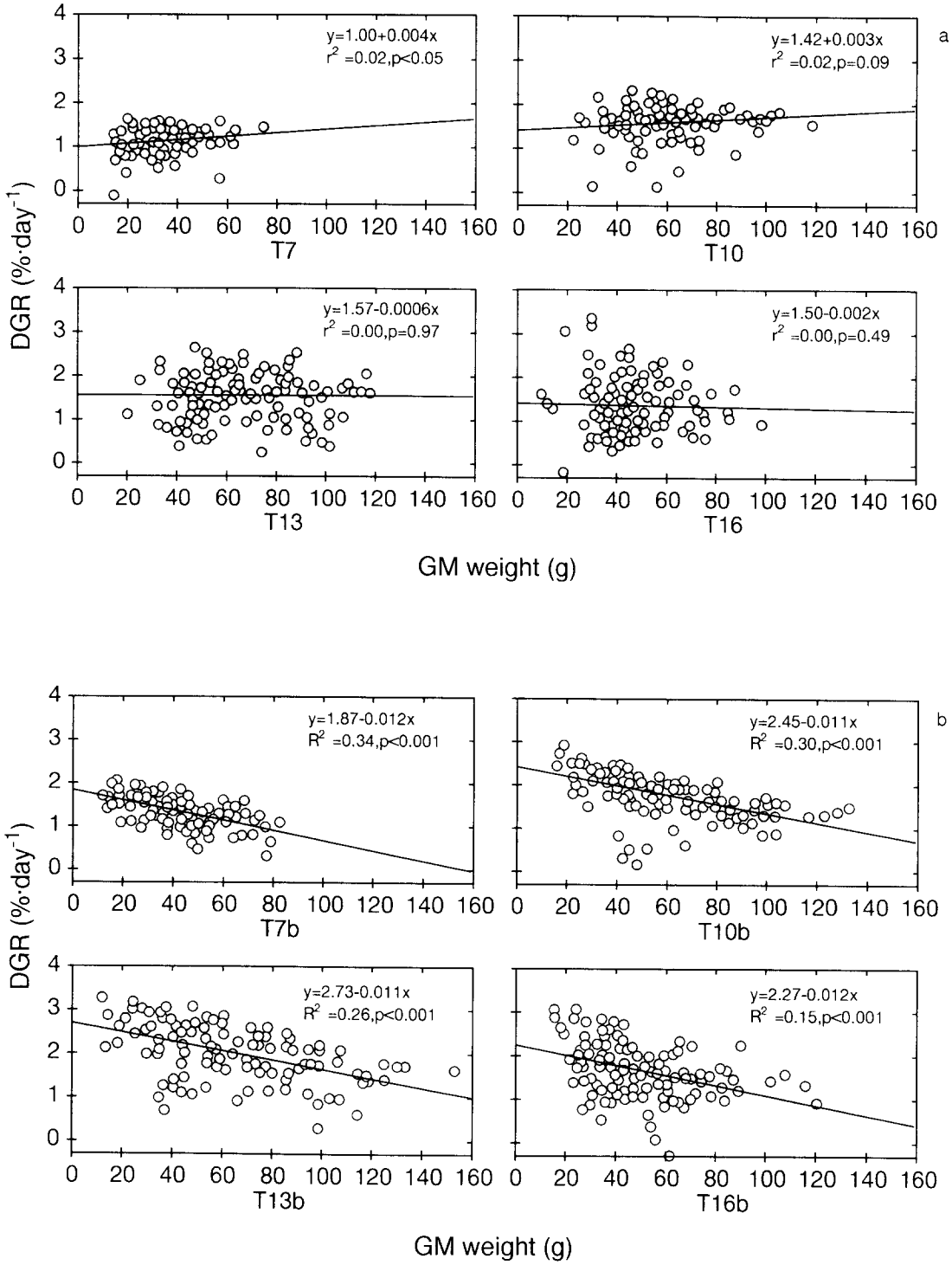

Fig. 2. Individual size-specific growth rate (DGR) *versus* geometric mean (GM) weight in a. Exp. 2 and b. Exp. 2b. Linear regression lines and corresponding equations, r^2 and p values for the slope, are given for each treatment.

halibut, although results from other fish species, mostly salmonids, do not suggest a negative effect of constant light. In fact, growth of juvenile Atlantic salmon is higher at LD24:0 than at LD21:3 during first feeding (Berg *et al.*, 1992). Further, temperature during the period January-March may have been too low for juvenile halibut to respond to the increase in photoperiod. Similar results are reported by Solbakken *et al.* (1994) for Atlantic salmon, where juveniles exposed to continuous light showed little or no increase in growth rate between January and April when temperature was low (5 to 6°C). As temperature increased, a positive growth response quickly became significant. At constant 12°C the response to continuous light was evident three weeks after initiation of the photoperiod treatment.

The relatively high size rank correlations observed in Experiments 2 and 2b are in accordance with the findings from mesocosm experiments with larval turbot (Rosenberg & Haugen, 1982). They used otolith microstructure to confirm that the large individuals tended to stay relatively large during the larval stage. Lower size rank correlations were observed in our experiments in the high temperature treatments, however, and this corresponded well with the higher variability in individual growth rates in these groups. We found no indication of the larger individuals within a group growing faster than the smaller ones throughout the experiment. This was evident as the general trend of constant or declining coefficient of variation (CV) of weight during the experiments. The declining CV was most likely due to the overall size effect on growth rate (Huston & DeAngelis, 1987). The relative size difference between the smaller and larger individuals decreased as DGR decreased with size.

The length-weight relationship for halibut indicates that a juvenile will have about half the weight at a given length compared to turbot juveniles (Sunde, 1993), due to its more elongated shape. Any effect this might have on obtainable or optimal densities of juvenile halibut in rearing tanks is unclear, but densities corresponding to 100 to 200% bottom cover are considered optimal for halibut larger than 2 kg (Björnsson, 1994). The weight-specific oxygen consumption is also somewhat higher for 80 g halibut juveniles than in similar-sized turbot juveniles (Imsland *et al.*, 1995). This is not surprising due to the higher temperature optimum for growth in turbot. The oxygen consumption values are also higher than in similar-sized plaice (*Pleuronectes platessa*), but lower than in flounder (*Platichthys flesus*) at 10 and 16°C (Fonds *et al.*, 1992). The relatively low oxygen consumption value commonly found in flatfish species is a beneficial trait in intensive rearing.

The results of the present experiment have important consequences for rearing of juvenile halibut. In order to enhance growth of the juvenile stages, temperature should be maintained at or above 10°C during the first winter and spring. Increasing temperatures up to or above 13°C has little or no positive effect on growth rate. As the halibut grows larger, temperature may be reduced to take advantage of the decrease in optimum temperature with increasing fish size.

Acknowledgements.—The authors would like to thank Stolt Sea Farm A/S for providing juvenile halibut for the experiments.

5. REFERENCES

Aune, A., G. Hole & K. Pittman, 1994. Growth in juvenile halibut (*Hippoglossus hippoglossus* L.) from 2-400 gms: a changing temperature optimum and some effects of light. Proc. Bordeaux Aquaculture, Mar. 23-25, 1994, Bordeaux, France: 61-62.

Berg, A., T. Hansen & S.O. Stefansson, 1992. First feeding of Atlantic salmon (*Salmo salar* L.) under different photoperiods.—J. appl. Ichthyol. **8:** 251-256.

Bergstad, O.A. & J.D.M. Gordon, 1993. First record of Atlantic halibut (*Hippoglossus hippoglossus* L.) larvae from the Skagerrak.—ICES J. mar. Res. **50:** 231-232.

Björnsson, B., 1993. Optimal temperature of immature halibut (*Hippoglossus hippoglossus* L.): effects of size. ICES C.M. 1993/F:37, 1:13.

——, 1994. Effects of stocking density on growth rate of halibut (*Hippoglossus hippoglossus* L.) reared in large circular tanks for three years.— Aquaculture **123:** 259-270.

Boehlert, G.W., 1981. The effects of photoperiod and temperature on laboratory growth of juvenile *Sebastes diplopora* and a comparison with growth in the field.—Fish. Bull. U.S. **79:** 789-794.

Brett, J.R., 1979. Environmental factors and growth. In: W.S. Hoar, D.J. Randall & J.R. Brett. Fish Physiology, Vol. VIII. Bioenergetics and growth. Academic Press, New York: 599-675.

Clarke, W.C., J.E. Shelbourn & J.R. Brett, 1978. Growth and adaptation to seawater in 'underyearling' sockeye (*Oncorhynchus nerka*) and coho (*O. kisutch*) salmon subjected to regimes of constant or changing temperature and day length.—Can. J. Zool. **56:** 2413-2421.

——, 1981. Effect of artificial photoperiod cycles, temperature and salinity on growth and smolting in underyearling coho (*Oncorhynchus kisutch*), chinook (*O. tshawytscha*) and sockeye (*O. nerka*) salmon.—Aquaculture **22:** 105-116.

Folkvord, A. & H. Otterå, 1993. Effects of initial size distribution, day length, and feeding frequency on growth, survival, and cannibalism in juvenile Atlantic cod (*Gadus morhua* L.).—Aquaculture **114:** 243-260.

Fonds, M., 1979. A seasonal fluctuation in growth rate of young plaice (*Pleuronectes platessa*) and sole (*Solea solea*) in the laboratory at constant temperatures and a natural daylight cycle. In: E. Naylor & R.G. Hartnoll. Cyclic phenomena in marine plants and animals. Pergamon Press, New York: 151-156.

Fonds, M., R. Cronie, A.D. Vethaak & P. van der Puyl, 1992. Metabolism, food consumption and growth of plaice (*Pleuronectes platessa*) and flounder (*Platichthys flesus*) in relation to fish size and temperature.—Neth. J. Sea Res. **29:** 127-143.

Hansen, E.H., 1990. Bruk av kunstig lys og lysmanipulering

for styrt produksjon av laksefisk. Ph.D. thesis, Institutt for elkraftteknikk, NTH, University of Trondheim: 1-137. (in Norwegian).

Haug, T., E. Kjørsvik & K. Pittman, 1989. Observations on a wild Atlantic halibut larvae, *Hippoglossus hippoglossus* (L.).—J. Fish Biol. **34:** 799-801.

Huston, M.A. & D.L. DeAngelis, 1987. Size bimodality in monospecific populations: a critical review of potential mechanisms.—Am. Nat. **129:** 678-707.

Imsland, A.K., A. Folkvord & S.O. Stefansson, 1995. Growth, oxygen consumption and activity of juvenile turbot (*Scophthalmus maximus* L.) reared under different temperatures and photoperiods.—Neth. J. Sea Res. **34:** 149-159.

Jobling, M., 1982. A study of some factors affecting rates of oxygen consumption of plaice, *Pleuronectes platessa* L.—J. Fish Biol. **20:** 501-516.

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

Øiestad, V. & L. Berg, 1989. Growth and survival studies of halibut (*Hippoglossus hippoglossus* L.) from hatching beyond metamorphosis carried out in mesocosms. In: N. De Pauw, E. Jaspers, H. Ackefors, & N. Wilkins. Aquaculture—a biotechnology in progress. European Aquaculture Society, Bredene, Belgium: 233-240.

Pethon, P., 1985. Aschehougs store fiskebok. H. Aschehoug & Co., Oslo: 1-447 (in Norwegian).

Prentice, E.F., D.L. Park, T.A. Flagg & S. McCutheon, 1986. A study to determine the biological feasibility of a new fish tagging system, 1985-1986. Dept. of Commerce, NOAA, NMFS, Northwest and Alaska Fisheries Centre, Seattle, WA: 1-89.

Rosenberg, A.A. & A.S. Haugen, 1982. Individual growth and size-selective mortality of larval turbot, *Scophthalmus maximus*, reared in enclosures.—Mar. Biol. **72:** 73-77.

Saunders, R.L., E.B. Henderson & P.R. Harmon, 1985. Effects of photoperiod on juvenile growth and smolting of Atlantic salmon and subsequent survival and growth in sea cages.—Aquaculture **45:** 55-66.

Schmidt-Nielsen, K., 1990. Temperature effects. In: K. Schmidt-Nielsen. Animal physiology: adaptation and environment, 4th ed. Cambridge University Press, New York: 218-221.

Sigurdsson, A., 1956. Contribution to the life history of the halibut at the west of Iceland in recent years (1936-1950).—Meddr Danm. Fisk.-og Havunders. **1** (16): 1-24.

Sokal, R.R. & F.J. Rohlf, 1981. Biometry. Second edition. W.H. Freeman & Co., San Francisco: 1-859.

Solbakken, V.A., T. Hansen & S.O. Stefansson, 1994. Effects of photoperiod and temperature on growth and parr-smolt transformation in Atlantic salmon (*Salmo salar* L.) and subsequent performance in seawater.—Aquaculture **21:** 13-27.

Stefansson, S.O., B. Björnsson, T. Hansen, C. Haux, G.L. Taranger & R.L. Saunders, 1991. Growth, parr-smolt transformation and changes in growth hormone of Atlantic salmon (*Salmo salar*) reared under different photoperiods.—Can. J. Fish. aquat. Sci. **48:** 2100-2108.

Stefansson, S.O., T. Hansen & G.L. Taranger, 1993. Growth and parr-smolt transformation of Atlantic salmon (*Salmo salar*) under different light intensities and subsequent survival and growth in sea cages.—Aquacult. Eng. **13:** 231-243.

Steffensen, J.K., 1989. Some errors in respirometry of aquatic breathers: how to avoid and correct for them.—Fish Physiol. Biochem. **6:** 49-59.

Sunde, L.M., 1993. Overlevelse og vekst hos ulike størrelsessorteringer av juvenil piggvar (*Scophthalmus maximus* L.) ved to temperaturer. Cand. scient. thesis., University of Bergen, Norway: 1-96. (in Norwegian).