# The interaction of temperature and fish size on growth of juvenile turbot

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Growth rate of tagged juvenile turbot was significantly influenced by the interaction of temperature and fish size. The results suggest the optimum temperature for growth of juvenile turbot in the size range 25–75 g is between 16 and 19° C. Optimal temperature for growth decreased rapidly with increasing size, and is between 13 and 16° C for 100 g turbot. Although individual growth rates varied highly at all times within the temperature treatments, significant size rank correlations were maintained during the experimental period. The study confirms that turbot exhibit ontogenetic variation in temperature optimum, which might partly explain different spatial distribution of juvenile and adult turbot in ocean waters.

## INTRODUCTION

Turbot *Scophthalmus maximus* Rafinesque is a marine demersal carnivorous bothid flatfish, that is relatively abundant in European waters from Iceland and Norway (68°N) to Morocco (30°N) (Blanquer *et al.*, 1992), including both the Mediterranean (Nielsen, 1986) and the Baltic Sea (Aneer & Westin, 1990). The total annual catch is less than 10 000 tonnes (Anonymous, 1994) and the stock shows signs of overexploitation (Weber, 1990). Declining catches, together with high commercial value and high growth rate in intensive culture has made turbot a promising candidate for marine fish culture. In the last decade, significant progress has been made in understanding the nutritional and environmental requirements of turbot (Jones *et al.*, 1981; Person-Le Ruyet *et al.*, 1991; Nijhof, 1994). Studies focused on the earlier life stages have demonstrated that high growth rates may be obtained over the temperature range from 10–20° C, with optimal temperature for growth around 18–19° C (Jones *et al.*, 1981; Danielssen *et al.*, 1990; Gaumet, 1994).

The combined effects of size and temperature on growth have been described for several fish species (Brett, 1979; Elliott, 1975; Fonds *et al.*, 1992; Buckel *et al.*, 1995; Hallaråker *et al.*, 1995). A downshift in temperature optimum with increasing size, i.e. ontogenetic shift, has been demonstrated in Atlantic cod *Gadus morhua* L. (Pedersen & Jobling, 1989), plaice *Pleuronectes platessa* L. (Fonds *et al.*, 1992), and Atlantic halibut *Hippoglossus hippoglossus* L.

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(Hallaråker *et al.*, 1995; Björnsson & Tryggvadóttir, 1996). In contrast, no shift in temperature optimum with increasing size was found in brown trout *Salmo trutta* L. (Elliott, 1975) nor in sockeye salmon *Oncorhynchus nerka* (Walbaum) (Brett *et al.*, 1969).

Fish generally have temperature ranges at which growth and survival are optimum (Brett, 1979; Gadomski & Caddell, 1991). These may differ with age and size as juveniles of many species prefer warmer temperatures than adults (McCauley & Huggins, 1979; Pedersen & Jobling, 1989). Early life history stages may also have different optimal temperatures, which may reflect field temporal and spatial distributions (Fonds, 1979; Gadomski & Caddell, 1991). Déniel (1990) reported that juvenile turbot stay in coastal waters, and migrate to deeper and cooler waters when reaching maturity. Other studies have confirmed that adult turbot migrate to deeper waters than do juvenile turbot (Aneer & Westin, 1990; Iglesias & Rodríguez-Ojea, 1994). An ontogenetic shift in optimal temperature (McCauley & Huggins, 1979) for growth has, thus, consequences for natural distribution of different life stages of that species as well as for rearing under culture conditions.

The following experiment was designed to investigate the effects of temperature and fish size, and their interaction, on growth rate of juvenile turbot, and attempts were made to estimate optimal temperatures for growth for fish of different sizes.

## MATERIALS AND METHODS

### FISH STOCK AND REARING CONDITIONS

Eggs from one female turbot were fertilized with pooled sperm from two males on 7 July 1991 and the eggs were incubated at 16° C. After hatching, the larvae were transferred to 8·0 m$^3$ plastic bags (van der Meeren, 1991) floating in a 53 000-m$^3$ seawater basin. From 16 July, the larvae were fed natural zooplankton filtered from the basin. After metamorphosis the juveniles were transferred to rearing tanks (1000 l) with a temperature of 13–16° C and fed a commercial dry diet. In October, the juveniles were brought to the Industrial Laboratory at the Bergen High Technology Centre and reared at 13° C under the natural light regime of Bergen (60°25′ N, 5°20′ E), until the start of the experiment.

The studies were carried out from 7 November 1991 until 26 May 1992, with various rearing groups terminated on different dates (see below). The 1-m$^2$ square, grey, covered fibreglass experimental tanks had a rearing volume of 400 l. Sea water with a salinity of 34·5 ± 0·2‰ was pumped from 90 m depth. Water flow was set initially at 20 l min$^{-1}$ for all experimental tanks. Oxygen saturation was measured weekly in the effluent water of all tanks and was above 85% at all times. The fish were attended once or twice daily, and these inspections included replacement of feed supply, removal of bottom water (20%) and monitoring of behaviour and mortality.

Light was provided by one 36-W fluorescent daylight tube installed in the tank cover. Photoirradiance at the tank bottom was approximately 4·2 µE m$^{-2}$ s$^{-1}$. A computer program generated a simulated natural light regime including twilight periods.

The fish were fed from automatic feeders every 4 min for 7 h each day. All groups were fed in excess, 3·0% of the biomass per day.

### EXPERIMENTAL DESIGN

On 7 November, the fish (*n*=800) were weighed and distributed randomly into eight tanks (100 in each tank). The fish had a mean weight (s.d.) of 7·2 (1·8) g on 7 November

and the mean weight of the treatment groups did not differ (two-way nested ANOVA, Power $(1 - \beta) > 0.9$). Fish were transferred from the holding temperature of 13° C directly to the four experimental temperatures of 10, 13, 16 and 19° C. Temperatures were measured twice daily, and remained within $\pm 0.2$° C of that prescribed. All groups were maintained under the natural photoperiod of Bergen (7 h light in mid-December, 18 h light in mid-May). All treatment groups consisted of two replicate tanks.

On 17 January (19° C) and 30 January (10, 13, 16° C), 40 randomly chosen fish from each experimental group (20 per tank) were tagged individually with Fisheagle® PIT tags (Prentice *et al.*, 1986). No fish died during tagging, but two fish died during the next 4 weeks. Additionally, two tags were lost/malfunctioned during the experiment. Due to technical failure of the electronic recording system it was not possible to detect tags on 26 March in the 10 and 16° C groups. In order to achieve overlapping size groups for all temperatures, the experiment was terminated on 9 April (19° C), 23 April (13, 16° C) and 26 May (10° C). All analyses reported in the present paper are based on data from the individually tagged fish.

## DATA ANALYSIS AND STATISTICAL METHODS

All fish were weighed individually to the nearest 0.1 g every 3 weeks in the period from 21 November to 4 January and every 2 weeks thereafter. Specific growth rate ($G$) was calculated according to the formula of Houde & Schekter (1981):

$$G = (e^g - 1)*100$$

where $g = (\ln W_2 - \ln W_1)(t_2 - t_1)^{-1}$ and $W$ is wet weight (g) at days $t_2$ and $t_1$, respectively. $G$ was regressed against geometric mean weight, $(W_1 * W_2)^{1/2}$ in the time interval. To avoid pseudoreplication, data for tagged fish ($n = 20$) in each tank were combined. The regression only included overlapping sizes (20–100 g). The growth rates during the first 2 weeks after tagging were not included in this analysis. In calculation of the temperature effect on growth rate, $Q_{10}$ of growth was calculated according to Schmidt-Nielsen (1990):

$$Q_{10} = (G_2/G_1)^{10/(t_2 - t_1)}$$

All statistical analyses were performed with STATISTICA® 4.1 (StatSoft, 1994). To assess normality of distributions a Kolmogorov–Smirnov test (Zar, 1984) was used, and homogeneity of variances was tested using the Levene's $F$-test (Brown & Forsythe, 1974). Individual growth trajectories were analysed using a growth curve analysis model (GCM, Timm, 1980; Chambers & Miller, 1995) which is an extension of the multivariate repeated measurements analysis of variance (MANOVA) model. The model equation of the GCM had the form:

$$Y(n \times p) = X(n \times q)B(q \times p) + E(n \times p)$$

where $Y(n \times p)$ are the growth at age vectors $y = (y_1, y_2, \ldots, y_p)$ for each $p$ (age) measurements on $n$ individual fish; $X(n \times q)$ is the design matrix or the set of extraneous variables measured for each individual, i.e. $q = age_p + group_i$; ($i = 10$, 13, 16 and 19° C); $B(q \times p)$ is the matrix of parameters estimated by the model; $E(n \times p)$ is the matrix of deviations for each individual from the expected value of $Y = XB$.

The $G$ v. geometric mean weight regressions were analysed using covariance analysis (ANCOVA, Sokal & Rohlf, 1995), the ANCOVA being run only for overlapping values of the covariate i.e. 20–100 g. The model equation of the ANCOVA had the form (Scheffé, 1959):

$$X_{ij} = \mu + a_i + \gamma(z_{ij} - \bar{z}) + \varepsilon_{ij}$$

where $\mu$ is the overall mean; $a_i$ is the treatment effect of the temperature groups; $\gamma$ is the regression coefficient for the $G$-geometric mean weight regression; $z_{ij}$ is the geometric mean weight of the fish (covariable); and $\varepsilon_{ij}$ is the error term.

Size ranking (initial size rank *v.* final size rank) was tested using Spearman's rank correlation (Zar, 1984). The effect of size on growth was analysed with a parabolic regression (Brett, 1979; Zar, 1984) where $G$ was regressed against temperature. The regression was made using the average growth rate of tagged fish at three sizes: 25–30, 45–50 and 70–75 g. An equal number of fish in each size range, and fish from the same size-class at each temperature, i.e. small or large, were used in the regressions. Optimal temperature for growth ($T_{opt.G}$) was calculated as the zero solution to the first derivative of the parabolic regression equations. Coefficient of variation of weight, CV=100* (s.d./mean weight), for each replicate tank (tagged fish, $n=20$) was regressed against weight and analysed with log regression ($Y=A_0+A_1 \log (X)$). Where $A_0$ and $A_1$ are constants, $Y$ is CV and $X$ is wet weight (Zar, 1984). Separate regressions were made for the four temperatures. The interactive effect of temperature and size on growth was analysed in a regression using the method of distance weighted least squares to estimate a three-dimensional response surface plot. Only geometric means of replicate tanks ($n=20$ in each) were used to avoid pseudoreplication. Data from the first 2-week period after tagging were omitted. The quadratic function fitted by this procedure (see Johnson & Wichern, 1992) had the general form:

$$Z=A_0+A_1X+A_2Y+A_3X^2+A_4Y^2+A_5(XY)$$

where $Z$ is the specific growth rate ($G$); $X$ is the natural logarithm of the geometric mean of weight (g); $Y$ is the temperature (° C); and $A_0$–$A_5$ are constants estimated by the model. Partial $r^2$ and $F$-values were calculated by dividing the partial sum of squares by the total sum of squares and the residual sum of squares, respectively. Data on mortality were tested in a $\chi^2$-test (Zar, 1984). A significance level ($a$) of 0·05 was used if not stated otherwise. In cases with non-significant statistical test, power ($1-\beta$) analysis for those tests were performed according to the methods described in Zar (1984) using $a=0.05$.

# RESULTS

## MORTALITY

In December, a bacterial infection, *Aeromonas sp.* was detected in the fish (O. M. Rødseth, Institute of Marine Research, Bergen, pers. comm.). Oral antibiotic treatment (*Flumequine*; 30 mg kg$^{-1}$ day$^{-1}$) was given from 13 to 18 December. Mortality was higher at 10° C (13%) than at 13° C (1·5%), 16° C (2·0%) and 19° C (2·0%). In this period, size-dependent mortality was found in the experimental group at 10° C as the dead fish were significantly smaller than the surviving fish (*t*-test). In contrast, total treatment mortality after tagging was 5% or less (Table I) and did not differ between treatments.

## GROWTH: EFFECT OF TEMPERATURE

From late January onwards, all groups showed different mean weights, the fish being successively larger from 10° C through 19° C (Table I). The 19° C group had the highest mean weight in early April (Table I). Mean individual growth trajectories were different (GCM, MANOVA$_{GROUPS}$, Wilk's lambda ($\Lambda$)$_{15, 406}$=0·18, $P<0.001$; Fig. 1) between the four temperatures from late January onwards. Significant differences were also found in growth at age trajectories of the experimental groups (MANOVA$_{GROUPS \times AGE}$, Wilk's $\Lambda_{12, 391}$=0·37, $P<0.001$; Fig. 1) from late January onwards. The fish at 10° C had the lowest growth of all groups until April, when only minor differences were found between the treatment groups (Fig. 1). $Q_{10}$ of overall specific growth rate of the tagged fish was 5·7 between 10 and 13° C, 1·1 between 13 and 16° C and 0·9

TABLE I. Average treatment characteristics in the experiment

| Temp. (°C) | Mean weight (g) | | | | | Coefficient of variation (weight) | | Survival (%) |
|---|---|---|---|---|---|---|---|---|
| | 17 Jan n=40 | 30 Jan n=40 | 9 April n=38–40 | 23 April n=38–40 | 26 May n=38 | 30 Jan n=2 | 9 April n=2 | |
| 10 | — | 13·7 ± 3·2$^d$ | 22·0 ± 5·6$^d$ | 25·5 ± 6·5$^c$ | 40·2 ± 8·1 | 22·9 ± 4·0$^b$ | 25·2 ± 1·7$^c$ | 95·0 |
| 13 | — | 21·0 ± 4·6$^c$ | 52·6 ± 11·0$^c$ | 62·9 ± 14·2$^b$ | — | 21·7 ± 3·4$^b$ | 20·8 ± 2·5$^c$ | 97·5 |
| 16 | — | 42·3 ± 10·4$^b$ | 113·9 ± 36·3$^b$ | 132·1 ± 43·2$^a$ | — | 24·6 ± 2·7$^b$ | 31·8 ± 2·9$^b$ | 100·0 |
| 19 | 44·5 ± 15·0 | 57·4 ± 19·3$^a$ | 151·4 ± 57·4$^a$ | — | — | 33·6 ± 1·9$^a$ | 37·9 ± 1·5$^a$ | 97·5 |

Results are given as mean ± S.D.
Weight data are given for 17 Jan (start 19° C), 30 Jan (start 10, 13 and 16° C), 9 April (termination 13 and 16° C) and 26 May (termination 10° C). Values not followed by the same letter are significantly different, with a as the highest value (Student's Newmans–Keuls test). Coefficient of variation (weight) is given for the two replicate tanks at each temperature.
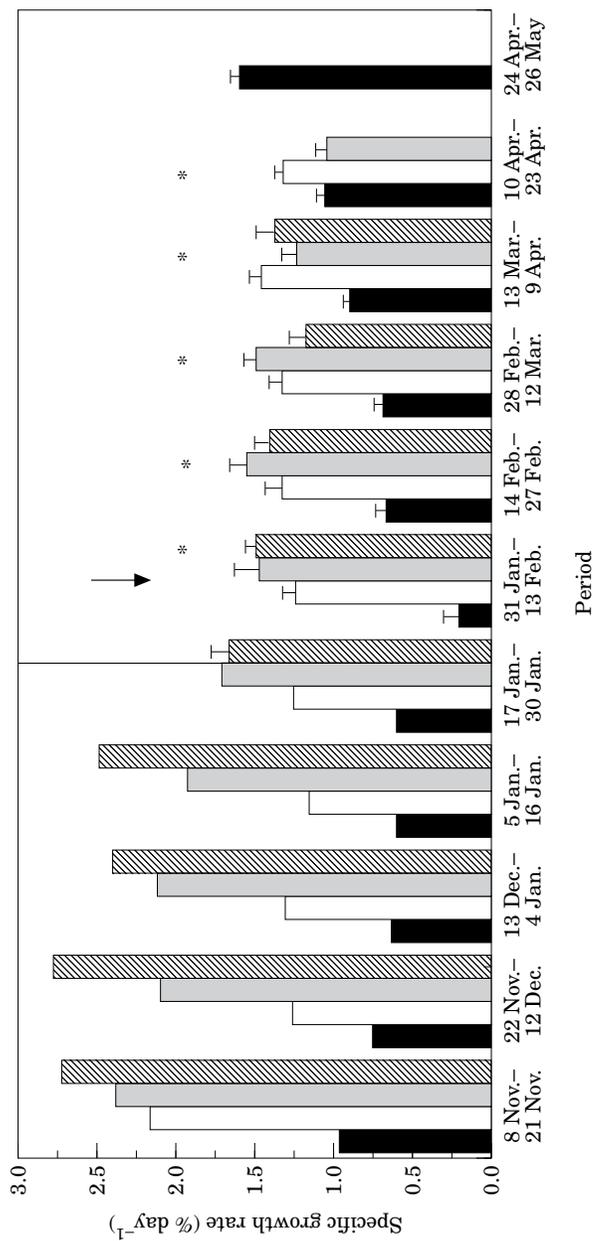
Fig. 1. Specific growth rates ($G$) during the experimental period. Data left of vertical line (untagged fish) were not used in the present study. ■, 10° C; □, 13° C; ◻, 16° C, ▨, 19° C. Vertical lines indicate standard error of mean (s.e.m.). Dates of tagging: 16 January (19° C) and 30 January (10, 13, 16° C). Arrow marks the first time period where temperature groups differ in growth rate (GCM MANOVA). *Significant difference in growth (tagged fish).
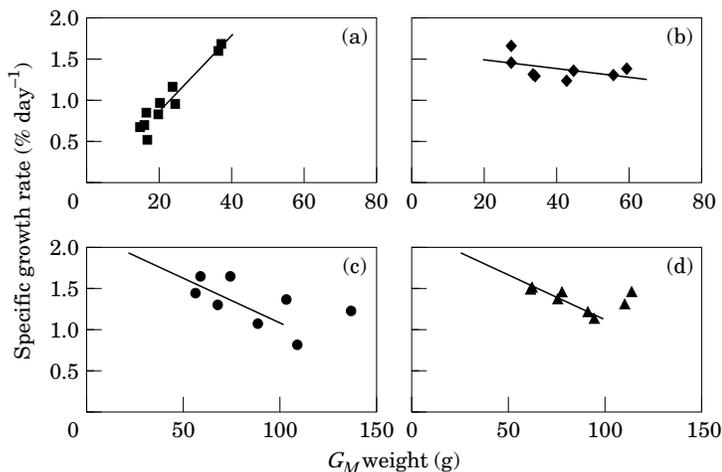
FIG. 2. Size-specific growth rate ($G$) *v.* geometric mean $G_M$ weight of juvenile turbot. Each datapoint is the mean of 20 individually tagged fish in a replicate tank. ■, 10° C, ◆, 13° C, ●, 16° C, ▲, 19° C. Regression analysis was made for overlapping sizes i.e. 20–100 g. The growth rates during the first 2 weeks after tagging were not included in this analysis. (a) 10° C: $G = -0.04 + 0.045 G_M$, $n=6$, $P<0.05$ (b) 13° C: $G=1.55 - 0.005 G_M$, $n=8$, $P=0.24$ (c) 16° C: $G=2.18 - 0.010 G_M$, $n=6$, $P=0.31$ (d) 19° C: $G=2.22 - 0.010 G_M$, $n=6$, $P<0.01$.

between 16 and 19° C. $Q_{10}$ between the various temperatures showed considerable variation between periods, and tended to be higher in February–March.

## GROWTH: EFFECT OF FISH SIZE

The size-specific growth rate differed between the treatment groups. At 10° C, growth rate increased [linear regression, $P<0.05$, Fig. 2(a)] with increasing weight, but at 19° C, growth rate declined [linear regression, $P<0.05$, Fig. 2(d)] with size. Growth declined with size at 13 and 16° C although this was not significant ($P>0.25$). The same trend of declining growth at high temperatures and increasing growth at lower temperatures was seen when growth rate was plotted against temperature for three size-classes of fish (25–30, 45–50 and 70–75 g; Fig. 3). The resulting parabolic regressions (Fig. 3) indicate that the temperature optimum for maximum growth changes with size. Overall, there was a significant interaction between temperature and size (ANCOVA, $P<0.01$, Table II).

## SIZE RANKING AND SIZE DISTRIBUTION

A significant size rank correlation (initial weight *v.* final weight) was maintained from January onwards at all temperatures (Spearman rank correlation, $r_s>0.65$, $P<0.01$, Fig. 4). The coefficient of variation (CV) of weight increased at 19° C (two replicate tanks) throughout the experimental period (log regression, CV$=15.74+4.44 \log W$, $r^2=0.83$, $P<0.01$, $n=8$). At the other temperatures, CV was stable or increased, although not significantly (16° C, $P>0.1$). Both initial (January) and final (April) CV were higher at 19 and 16° C compared to 10 and 13° C (Table I).
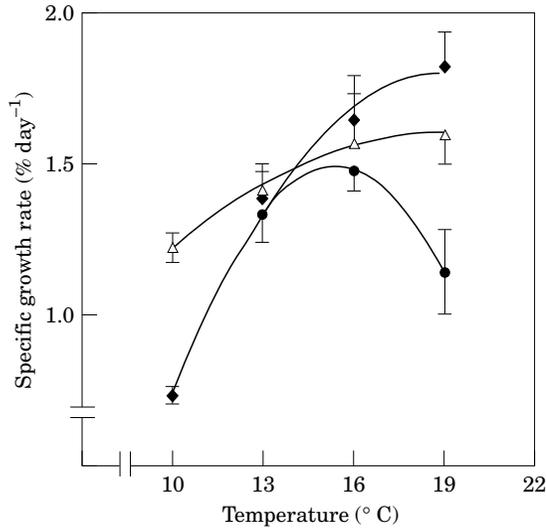
FIG. 3. Changes in growth rate with temperature for three different sizes of juvenile turbot. The lines represent the least squares second-order polynomial fit to the data: $G = aT^2 + bT + c$ where $G$ = specific growth rate, $T$ = temperature, and $a$, $b$ and $c$ are constants determined by the regression. Vertical lines indicate standard error of mean. ◆ 25–30 g; $G = -0.013T^2 + 0.487T - 2.854$, small fish, $n = 10$ for each point. △ 45–50 g; $G = -0.005T^2 + 0.182T - 0.061$, large fish, $n = 20$ for each point. ● 70–75 g; $G = -0.012T^2 + 0.392T - 1.800$, large fish, $n = 20$ for each point.

TABLE II. Analysis of covariance (ANCOVA) for the regression of specific growth rate ($G$, % day$^{-1}$) against geometric mean weight ($W$, g wet weight) at different temperatures ($T$, °C)

| Source of variation | Sum of squares | d.f. | Mean square | $F$-ratio | $P$ |
|---|---|---|---|---|---|
| Main effect | | | | | |
|   Temperature ($T$) | 0·105 | 3 | 0·035 | 0·837 | 0·49 |
| Covariate | | | | | |
|   Geometric mean weight ($W$) | 0·078 | 1 | 0·078 | 1·876 | 0·18 |
| Interaction | | | | | |
|   $T \times W$ | 0·467 | 3 | 0·155 | 8·054 | <0·01 |
| Residual | 0·756 | 18 | 0·042 | | |

d.f., degrees of freedom.

The ANCOVA is run for overlapping sizes (20–100 g). Data from the first period after tagging are not included in the analysis.

## GROWTH: THE INTERACTION BETWEEN TEMPERATURE AND FISH SIZE

The combined effects of fish size and temperature on growth, based on all data for the tagged fish (replicate tanks, $n = 2$), were described by the response surface given by the quadratic function (distance weighted least squares method):

$$G = -7.38 + 4.05X + 0.11Y - 0.32X^2 + 0.01Y^2 - 0.10(XY),$$
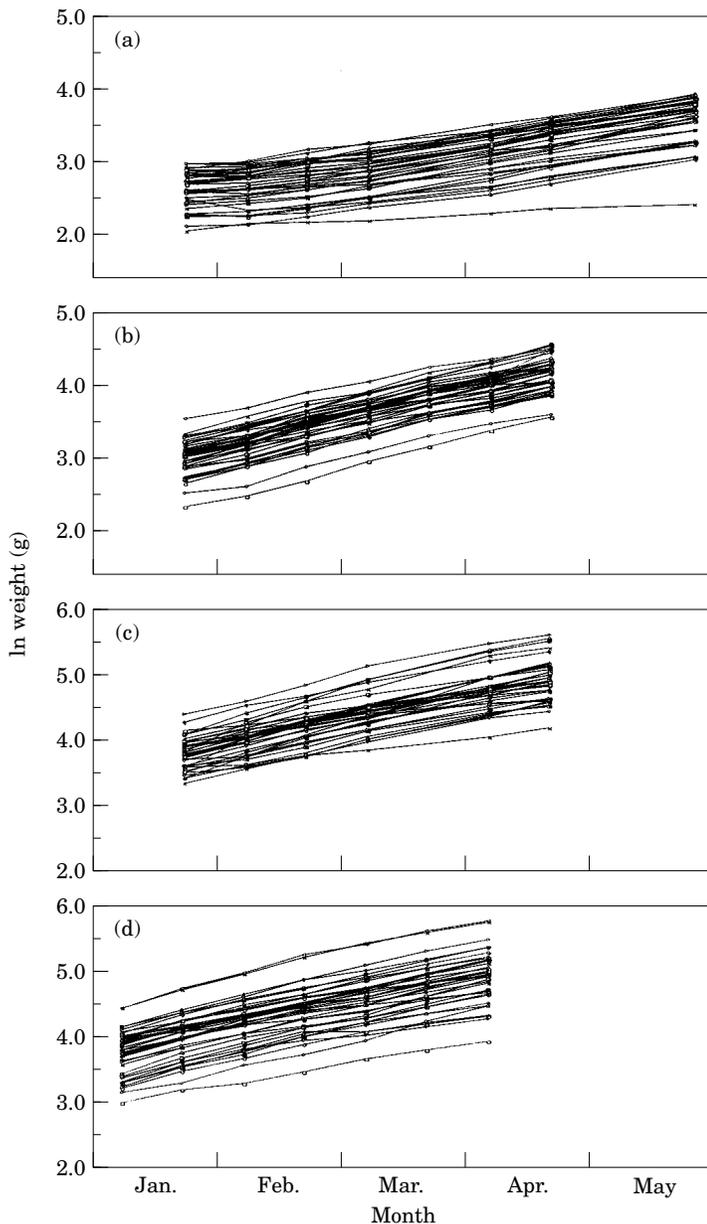$$n = 34, \ r^2 = 0.78, \ P < 0.01 \tag{1}$$

FIG. 4. Individual growth trajectories for tagged juvenile turbot during the experiment. Data for replicate tanks are presented together. Due to technical failure results from 10 and 16° C treatment groups were omitted on 27 March. The results of Spearman's rank correlation for size rank at start and final size rank are given. (a) 10° C: $r_s > 0.90$, $P < 0.01$, $n = 38$; (b) 13° C: $r_s > 0.75$, $P < 0.01$, $n = 39$; (c) $r_s > 0.65$, $P = 0.01$, $n = 40$; (d) 19° C: $r_s > 0.85$, $P < 0.01$, $n = 39$.

where $X$ is ln of geometric mean weight, and $Y$ is temperature. The response to temperature changed with size, with almost a linear relationship between growth and temperature at small sizes (Fig. 5). As the fish grew larger the contrary
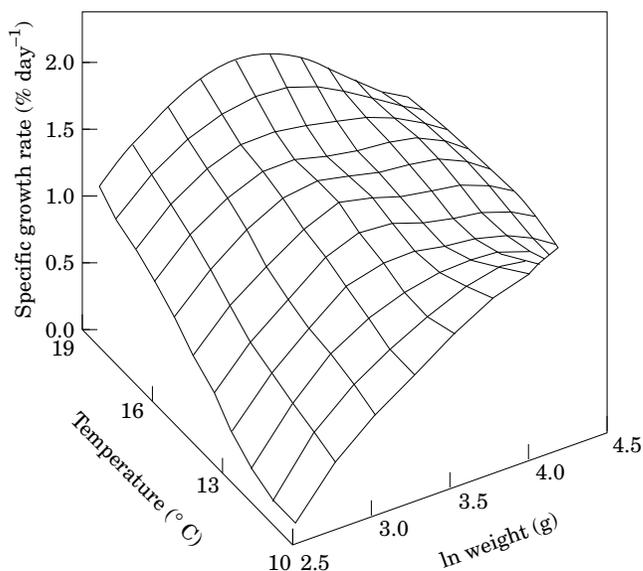
FIG. 5. Response surface for specific growth rate of juvenile turbot between 12 and 90 g. Lines are marked every 0·9° C and ln (8 g) interval. The surface represents the distance weighted least squares fit of the quadric function: $Z = A_0 + A_1X + A_2Y + A_3X^2 + A_4Y^2 + A_5XY$, where $Z$ is specific growth rate, $X$ is ln of the geometric mean weight, and $Y$ is temperature. All coefficients except $A_2$ are significant at the $P < 0.05$ level, and the quadric function is highly significant ($F_{5, 28} = 26.8$, $P < 0.01$, $r^2 = 0.78$).

trend, however, was found (Fig. 5) as better growth was observed at the lower temperatures (10 and 13° C) compared to the highest temperature.

## DISCUSSION

Growth rate of juvenile turbot was significantly influenced by temperature and fish size (Figs 2, 3 and 5). Overall growth rate was highest at 19° C. However, at 13 and 16° C, growth rate was equal or higher in the later stages of the experiment, while the fish at 10° C showed overall significantly lower growth rates (Fig. 1). This is in accordance with earlier studies on turbot (Jones *et al.*, 1981; Gaumet, 1994; Imsland *et al.*, 1995). Jones *et al.* (1981) found the temperature for maximum growth of juvenile turbot to be 18·9° C and the temperature for maximum food conversion efficiency to be 16·2° C, but they pointed out the possibility of a different temperature optimum for fish larger than 30 g. Gaumet (1994) reared juvenile turbot at 11, 14, 17 and 20° C, and reported best growth at 17° C, with only small differences in growth between 14 and 20° C.

Further, growth rate of juvenile turbot was significantly influenced by size (Figs 2 and 5). This is in accordance with previous studies on several fish species (Elliott, 1975; Brett, 1979, Pedersen & Jobling, 1989; Fonds *et al.*, 1992; Rijnsdorp, 1993; Björnsson & Tryggvadóttir, 1996) that have highlighted fish size as an important factor influencing growth rate. The results of parabolic regressions (Fig. 3) suggest the optimum temperature for growth

($T_{opt.G}$) for juvenile turbot in the size range 25–75 g is between 16 and 19° C. This is in accordance with Jones *et al.* (1981), who calculated 18·9° C as $T_{opt.G}$ for 5–30 g turbot, and Scherrer & Person-Le Ruyet (unpublished) who suggested $T_{opt.G}$ for 6–20 g turbot to lie between 16 and 19° C. The decreasing $T_{opt.G}$ with size (Figs 3 and 5) is in accordance with studies on Atlantic halibut (Hallaråker *et al.*, 1995; Björnsson & Tryggvadóttir, 1996). The high growth rates over a relatively wide temperature range in turbot are of interest for commercial aquaculture. Moreover, the parabolic regressions (Fig. 3) flatten out with increasing size in accordance with earlier studies (Brett *et al.*, 1969; Elliott, 1975; Björnsson & Tryggvadóttir, 1996). Growth comparisons of different size fish were done at different times and therefore at different photoperiods. However, as earlier studies on juvenile turbot have not revealed any significant effect of different photoperiods on growth of juvenile turbot (Imsland *et al.*, 1995), valid comparisons can be made.

The decrease in $T_{opt.G}$ with fish size, as observed for juvenile turbot, has also been reported for Atlantic cod (Pedersen & Jobling, 1989), plaice (Fonds *et al.*, 1992), Atlantic halibut (Hallaråker *et al.*, 1995; Björnsson & Tryggvadóttir, in press), and has been demonstrated for fish in general (Cuenco *et al.*, 1985). The model of Cuenco *et al.* (*op cit.*) predicts a shift of about 1–2° C in $T_{opt.G}$ with increasing weight in the range of 10–500 g which is lower than found in this study, where a shift of approximately 3° C in $T_{opt.G}$ with increasing weight in the range of 25–75 g is calculated (Fig. 3), and a similar shift indicated from 12–90 g (Fig. 5). In contrast, no shift in $T_{opt.G}$ with size was found in sockeye salmon (1–190 g; Brett, 1979) nor in brown trout (10–300 g; Elliott, 1975).

Increasing temperature from 10 to 13° C gave the highest overall increase in growth rate calculated as $Q_{10}$ ratio, while $Q_{10}$ between 13 and 16° C was 1·1 suggesting little positive effect of further increasing temperature for culture of juvenile turbot from 13 to 16° C. Overall $Q_{10}$ was <1·0 between 16 and 19° C, indicating that temperature was above the optimum for the size range studied. Further, size dependent growth was significantly influenced by temperature (Figs 2 and 5). There was an inverse relation between the slopes of the size *v.* growth rate regressions and temperature, with a significant positive slope at 10° C and significant negative slope at 19° C (Fig. 2). The increase in growth rate with increasing size at lower temperatures indicates that the optimum temperature for growth was shifted downwards as the fish grew larger, in accordance with the findings of Fonds *et al.* (1992) and Hallaråker *et al.* (1995). This further agrees with the general pattern suggested by Brett (1979).

Many fish species thermoregulate behaviourally, i.e. seek out a temperature close to their optimal temperature for growth (Zinichev & Zotin, 1987; Hill & Magnuson, 1990; Wildhaber & Crowder, 1990). Hence, temperature preferenda of the fish will tend to coincide with the optimal temperature for growth (Hill & Magnuson, 1990; Gadomski & Caddell, 1991). In their review of the ontogenetic effects on thermal preferenda of fish, McCauley & Huggins (1979) concluded that, in some fishes, there were shifts in temperature preferenda towards lower temperatures for larger fish. Little is known about distribution and temperature preferences of wild juvenile turbot. The studies of Jones (1973), Aneer & Westin (1990), Déniel (1990), and Iglesias & Rodríguez-Ojea (1994) indicate that turbot are found in shallow water during late spring and

summer, but migrate into deeper water during autumn and winter. Their studies also indicate that mature turbot undergo longer migrations and have different spatial distributions than do juveniles. The downshift in temperature optimum with size found in the present study is thus in accordance with the findings of adult turbot in deeper and cooler water compared with juvenile turbot (Déniel, 1990; Inglesias & Rodríguez-Ojea, 1994) in ocean waters. Different spatial distributions of early life stages and adults as a consequence of different optimum temperatures have been reported for some fish species (Fonds, 1979; Gadomski & Caddell, 1991), and efforts have been made to predict distribution of fish based on the optimal temperature for growth (Bryan *et al.*, 1990).

The high size rank correlations (Fig. 4) observed at all temperatures are in accordance with the findings from mesocosm experiments with larval turbot (Rosenberg & Haugen, 1982; Danielssen *et al.*, 1990). Using otolith microstructure from turbot to calculate individual growth trajectories, they confirmed that the large individuals maintained their position relative to each other during the larval stage. Significant size rank correlations have also been observed in studies with tagged juvenile halibut (Hallaråker *et al.*, 1995). The results from present study indicate that larger individuals within each temperature do not grow faster than the smaller ones, and that the individuals maintain their relative size position throughout the experimental period. These findings may indicate the early establishment of a stable size ranking, which is common under culture conditions (Purdom, 1974; Rosenberg & Haugen, 1982; Westerhagen, 1983; Economou *et al.*, 1991). Explanations of the stable size ranking in the present study might be heritable individual growth differences (Huston & DeAngelis, 1987) or sex-related growth differences (Devauchelle *et al.*, 1988; Imsland *et al.*, 1996). Imsland *et al.* (1996) reported significant growth differences between male and female turbot from 9 months posthatch. The higher CV of weight seen at 16 and 19° C compared to 10 and 13° C might be due to a combination of size (Carmichael, 1994) and growth effects, reflecting differing growth rates among individuals (Wright & Huntingford, 1993), as the fish at 16 and 19° C were larger in January (Table I) and grew faster from January to March (Fig. 1).

## CONCLUSIONS

The present study confirms that turbot exhibit ontogenetic variation in temperature optimum. Further, the results from the present experiment have important consequences for rearing of juvenile turbot. As the turbot grows larger, temperature may be reduced to take advantage of the change in optimal temperature for growth with increasing fish size. Also, this species exhibits a high growth rate over a large temperature interval, which may be important in turbot aquaculture.

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