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Effects of exposure to extended photoperiods during the first winter on long-term growth and age at first maturity in turbot (*Scophthalmus maximus*)

Albert K. Imsland *, Arild Folkvord, Ólöf D.B. Jónsdóttir, Sigurd O. Stefansson

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

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Abstract

The effects of photoperiod on growth of juvenile turbot and the consequences of extended daylength on age at first maturation were investigated. Growth of individually tagged turbot (initial weight 34–44 g, $n = 94$) was monitored for 18 months. The fish were held under natural photoperiod from hatching (July) until the start of the experiment in December. From December 4, 1991 until May 26, 1992, the fish were reared under constant light (LD24:0, $n = 27$), 16-h light:8-h darkness (LD16:8, $n = 35$), or simulated natural photoperiod for 60°25′N (LDN, $n = 32$). The fish were then reared together on LDN for 12 months until first maturation during summer 1993 (age 24 months). The fish were held at 16°C from December 1991 onwards. A growth promoting effect of extended daylength was seen in the LD16:8 and LD24:0 groups, but the effect was not apparent in the LD24:0 group until 6 months after the fish had been transferred to LDN. The final mean weights of the female turbot were 1727 g and 1777 g in the LD16:8 and LD24:0 groups, respectively, whereas final mean weights of males in these groups were 1075 g and 1055 g. In the LDN group the final mean weights for females and males were 1290 g and 909 g, respectively. The results from the present study suggest that exposure to extended photoperiod alters the growth pattern of both maturing fish and immature fish resulting in increased overall growth. Fewer males matured in the LD16:8 (26%) and LD24:0 (17%) groups than in the LDN (56%) group, whereas there were no differences between the experimental groups in the proportion of females that matured (range = 60–63%). It is concluded that extended daylength

* Corresponding author. Tel.: +47-55-58-44-71; fax: +47-55-58-44-50; e-mail: albert.imsland@ifm.uib.no.

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during the first winter influences both the long term growth pattern and the age at first maturity of turbot. © 1997 Elsevier Science B.V.

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1. Introduction

The culture of turbot (*Scophthalmus maximus* Rafinesque) has developed rapidly in Europe in the last decade, with production increasing from 4 metric tons in 1984 to 3000 metric tons in 1995 (Josupeit, 1996). Several studies have been carried out to investigate the effects of temperature on growth rates (see Nijhof, 1994), but information about the effects of other environmental factors, such as photoperiod, on growth and age at first maturity is scarce. Exposure to extended photoperiods (beyond the natural daylength) has been shown to lead to increased growth rates in salmonids (Saunders and Henderson, 1970; Clarke et al., 1981; Stefansson et al., 1991; Hansen et al., 1992), centrarchids (Gross et al., 1965), ictalurids (Kilambi et al., 1970), scorpaenids (Boehlert, 1981), siganids (Duray and Kohno, 1988), gadoids (Folkvord and Otterå, 1993), and marine flatfish (Fonds, 1979; Hallaråker et al., 1995; Holm, 1995; Imsland et al., 1995). Photoperiod is also generally accepted as being the most important factor synchronizing sexual maturation and reproduction in fish in temperate regions (Scott, 1979; Bromage et al., 1993). In salmonids altered photoperiod regimes may affect both the age at which fish reach first sexual maturity and the timing of maturation within the annual cycle (Duston and Bromage, 1988; Kråkenes et al., 1991; Hansen et al., 1992; Taranger, 1993). Constant light in winter may be used to delay maturation in Atlantic salmon (Hansen et al., 1992; Taranger, 1993), and in turbot culture photoperiod manipulation is used to produce eggs and sperm on a year-round basis (Fores et al., 1990; Stoss and Røer, 1993). Studies on the effects of photoperiod manipulation on growth and age at first maturity in turbot are, however, lacking.

The present experiment was carried out to investigate the effect of photoperiod on growth of juvenile turbot during their first winter and to examine the subsequent effects of extended daylength on age at first maturity.

2. Materials and methods

2.1. Fish material and rearing conditions

Eggs from one female turbot were fertilised with the pooled sperm from two males on July 7, 1991. After hatching the larvae were transferred to 8.0 m^3 plastic bags floating in a sea water basin at Selvåg just south of Bergen (Jakobsen, 1985), and from July 16 the larvae were fed natural zooplankton filtered from the basin. After metamorphosis the juveniles were transferred to indoor rearing tanks (1000 l), with flow-through sea water at 13–16°C and were fed a commercial dry diet. The larvae and juveniles were reared under the natural light regime of Bergen (60°25′N, 5°20′E) from hatching until they were brought to the laboratory.

In October 1991, the juveniles were brought to Bergen High Technology Centre, where they were reared at 13°C under a simulated natural light regime of Bergen until the start of the experiment. The studies were carried out from November 7, 1991 until June 15, 1993. Initially, the fish were held in 1-m^2 tanks, but they were later moved to 7-m^2 circular tanks. Each tank was supplied with 20 l min^{-1} of sea water with a salinity of 34.5 ± 0.2‰. Oxygen saturation was above 75% at all times. Between January and May 1992 the fish were fed using automatic feeders timed to distribute food every four minutes during the photophase. From June 1992 onwards the fish were fed twice a day. Commercial dry feed (Marine pellets 2–9 mm; Felleskjøpet AS, Bergen) was provided in excess, the amounts fed being adjusted after each weighing according to recent growth rate (feeding per day = previous growth rate × biomass in tank). For further information concerning details of fish and the larval rearing see Imsland et al. (1995, 1997).

2.2. Experimental design

Based on the knowledge of the life history (e.g. Jones, 1973; Déniel, 1990) and earlier experiments on this species (e.g. Jones et al., 1981) 16°C was used as the rearing temperature, and three light regimes were chosen. On November 7, 1991 temperature was adjusted from 13°C to 16°C. Thereafter temperature was measured daily, and it remained at 16 ± 0.2°C throughout the experiment. On December 4, three light regimes were established (Fig. 1). One group remained on natural photoperiod (LDN) for Bergen. The two other photoperiods were 16-h light: 8-h darkness, LD16:8, and constant light, LD24:0. There were 100 fish in each tank with two replicate tanks for each photoperiod group. Light was provided by one 36 W fluorescent daylight tube installed in the tank cover. Photoirradiance at the tank bottom was approximately 4.2 μmol m^{-2} s^{-1}. A computer program (Hansen, 1990) generated a simulated natural light regime including twilight periods.

On January 30, 1992 a total of 94 randomly chosen fish from the experimental groups (LDN, $n = 32$; LD16:8, $n = 35$; LD24:0, $n = 27$) were individually tagged with Fisheagle® PIT tags (Prentice et al., 1986). Initial weight at tagging ranged from 34–44 g (Table 1). All growth analyses are based on these fish (42 females and 52 males). From

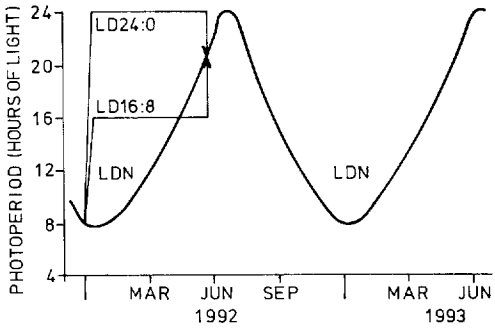

Fig. 1. Photoperiods employed in the experiment. LDN (simulated natural photoperiod of Bergen, 60°25′N, 5°20′E), LD16:8 (16-h light:8-h darkness), LD24:0 (continuous light). From May 1992 onwards all groups were reared on LDN in a common rearing environment until June 1993.

Table 1
Mean weights (g) for all experimental categories at selected dates throughout the study

Variable			January 30 1992	April 24 1992	July 3 1992	October 3 1992	December 3 1992	February 3 1993	April 3 1993	June 15 1993
Females, maturation status			n.s.	n.s.	n.s.	n.s.	n.s.	$P < 0.05$	$P < 0.05$	$P < 0.05$
Females, photoperiod treatment			n.s.	n.s.	$P < 0.01$	$P < 0.05$	n.s.	n.s.	n.s.	n.s.
Males, maturation status			n.s.	n.s.	n.s.	$P < 0.05$	$P < 0.01$	$P < 0.01$	$P < 0.01$	$P < 0.01$
Males, photoperiod treatment			n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	$P < 0.05$	$P < 0.05$
	Grouping	n								
Females	LDN-M	10	42 (3)	130 (11)	237 (27)^{a,b}	547 (60)^{a,b}	787 (85)	973 (102)^{a,b}	1211 (160)^{a}	1288 (140)^{a}
	LD16:8-M	10	44 (4)	150 (11)	257 (20)^{a,b}	616 (47)^{a}	961 (84)	1222 (111)^{a}	1721 (174)^{a}	1929 (216)^{a}
	LD24:0-M	6	42 (2)	114 (13)	188 (16)^{b}	497 (51)^{a,b}	806 (97)	1127 (151)^{a,b}	1650 (240)^{a}	1995 (267)^{a}
	LDN-IM	6	38 (3)	135 (20)	297 (43)^{a}	664 (83)^{a}	902 (100)	988 (117)^{a,b}	1079 (120)^{a}	1119 (192)^{a}
	LD16:8-IM	6	34 (3)	100 (11)	225 (20)^{a,b}	552 (98)^{a,b}	830 (134)	1018 (174)^{a,b}	1355 (263)^{a}	1391 (182)^{a}
	LD24:0-IM	4	39 (4)	111 (11)	160 (11)^{b}	363 (32)^{b}	537 (32)	668 (45)^{b}	1008 (56)^{a}	1156 (131)^{a}
Males	LDN-M	9	42 (2)	139 (12)	236 (24)	512 (46)^{a}	718 (67)^{a,b}	766 (65)^{a}	974 (75)^{a,b}	1007 (52)^{a,b}
	LD16:8-M	5	34 (2)	108 (6)	250 (27)	553 (46)^{a}	796 (88)^{a,b}	1003 (117)^{a}	1322 (129)^{a}	1378 (102)^{a}
	LD24:0-M	3	41 (4)	141 (4)	242 (31)	561 (61)^{a}	877 (95)^{a}	1007 (110)^{a}	1336 (148)^{a}	1474 (141)^{a}
	LDN-IM	7	39 (3)	119 (7)	236 (20)	436 (29)^{a}	613 (49)^{a,b}	672 (58)^{a}	782 (61)^{b}	796 (76)^{b}
	LD16:8-IM	14	36 (1)	125 (6)	242 (15)	478 (33)^{a}	642 (53)^{a,b}	740 (60)^{a}	947 (63)^{a,b}	966 (69)^{a,b}
	LD24:0-IM	14	40 (3)	115 (10)	194 (17)	362 (42)^{a}	547 (61)^{b}	696 (81)^{a}	985 (102)^{a,b}	1040 (89)^{a,b}

Results are given as mean (standard error of mean); n = number of fish in each grouping category. Results (two-way ANOVA, $P < 0.05$) for the main effects (maturation status, photoperiod treatment) are given for each date. The interaction between maturation status and photoperiod treatment was never significant. Separate analyses were made for each sex

^{a,b}Different letters indicate statistical differences (in cases of significant ANOVAs) with ^{a} as the highest value within each sex (Student–Newmans–Keuls test, $P < 0.05$).

Non-significant results are marked n.s. Vertical line indicates period of different photoperiods.

Abbreviations: M = mature, IM = immature.

January to May the tagged fish were reared in two replicate tanks for each photoperiod treatment. On May 26, 1992 the experimental photoperiods LD16:8 and LD24:0 were discontinued, and all fish from there were then reared in the same tank under LDN (Fig. 1).

Sexual maturation was assessed by palpation of the abdomen of the fish at all weighing times in 1993, and fish were examined for running milt or roe. In June 1993, all fish within each experimental group were classifed to one of four categories based on maturation status, i.e., maturing females, maturing males, immature females and immature males. Further, biopsy samples were taken from immature fish to determine the sex of these individuals. Six randomly chosen tagged fish (two from each photoperiod treatment) were sacrificed in gonad sampling in April 1993 (data not used in the present study).

2.3. Calculations and statistical methods

Weighing was conducted every two weeks until May 26, 1992, monthly until August 1992 and every two months thereafter. Fish were weighed individually to the nearest 0.1 g. The fish were not starved before weighing. Specific growth rate (SGR) was calculated according to the formula of Houde and Schekter (1981):

$$\mathrm{SGR} = (e^{g} - 1)100\%$$

where $g = (\ln(W_2) - \ln(W_1))(t_2 - t_1)^{-1}$ and W_2 and W_1 are weights on days t_2 and t_1, respectively.

Statistical analyses were performed with STATISTICA™ 4.1 (StatSoft, 1994), and GLIM™ 3.77 (Payne, 1987). A Kolmogorov–Smirnov test (Zar, 1984) was used to assess for normality of distributions. The homogeneity of variances was tested using the Levene F-test (Zar, 1984). The mean weights of the experimental groups on different dates were tested in a one-way Model I analysis of variance (ANOVA); separate analyses were performed for females and males. Significant ANOVAs were followed by a Student–Newman–Keuls multiple comparison test to determine differences among experimental groups. Mean individual growth trajectories for females and males in each experimental group were analysed using a growth curve analysis model (GCM, Timm, 1980; Chambers and Miller, 1995) which is an extension of the multivariate repeated measurements analysis of variance (MANOVA) model. The differences in mean weights between mature and immature fish within the photoperiod treatments were tested in a Model I two-way ANOVA (Zar, 1984). Separate tests were performed for each sex.

The variance–covariance structure of the growth data was analysed with a two component factor analysis (Johnson and Wichern, 1992; StatSoft, 1994). In this analysis the growth rate and size rank of each individual throughout the experiment were used as variables. The purpose of the analysis was to reduce the original variables to two linear combinations (principal components) that accounted for as much as possible of the total variation of the original variables (Johnson and Wichern, 1992). The factor loadings of the two-factor solution were tested in a one-way MANOVA (Johnson and Wichern, 1992).

Data on maturity proportions between the sexes were tested in a 2 (females, males) × 2 (mature, immature) contingency-table chi-square test and maturity propor-

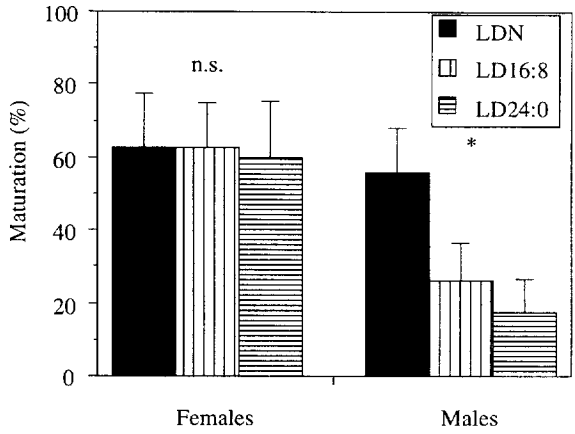

Fig. 2. Proportions of maturing two-year old female and male turbot reared under three different photoperiod regimes. Vertical line indicates binomial standard deviation [$SD(x) = \sqrt{npq}$]. $^{*}P < 0.05$; n.s. $P > 0.7$ (χ^2 test).

tions within each photoperiod group were tested in a 3 (LDN, LD16:8, LD24:0) × 2 (mature, immature) contingency-table chi-square test (Zar, 1984). Logistic regression (Hosmer and Lemeshow, 1989) was used to analyse which of the factors (sex, photoperiod regime, and the covariat size measured in April 1993) influenced the state of maturation (mature or immature) of individual fish. Several models were fitted using the GLIM® 3.77 statistical package (Payne, 1987), employing a binominal error distribution. This test is an analogue to analysis of covariance with a continuous variable. A significance level (α) of 0.05 was used if not stated otherwise. In non-significant cases, power ($1 - \beta$) analyses were performed according to the methods described in Zar (1984) and Hosmer and Lemeshow (1989) using $\alpha = 0.05$.

3. Results

3.1. Factors influencing maturation

Overall, 45.7% of the fish matured in 1993 (Fig. 2). Maturity proportions differed between sexes (2 × 2 contingency-test, $\chi^2 = 8.0$, $P < 0.025$). Further, the proportion of mature males differed between the photoperiod groups, with significantly fewer males maturing in the LD16:8 (5 out of 19, 26%) and LD24:0 (3 out of 19, 17%) groups (3 × 2 contingency-test, $\chi^2 = 6.2$, $P < 0.05$, Fig. 2) than in the LDN (9 out of 16, 56%) group. The proportions of mature females did not differ between photoperiods. Based on the logistic regression models (Table 2), maturation appeared to be mainly related to body weight ($G = 15.58$, $P < 0.001$, Table 2), and photoperiod regime ($G = 8.03$, $P < 0.005$, Table 2). There were no significant interactions between sex, size and photoperiod regime ($P > 0.08$, power $(1 - \beta) > 0.9$).

Table 2
Logistic regression of maturity (y) in individually tagged female and male turbot as a function of body size in April 1993 (W in g) the main factors sex (S) and photoperiod regime (PR), and the interaction between sex, photoperiod regime and body size. Estimated logistic regression coefficients/SE, scaled deviance, the likelihood ratio test statistic (G), and the P value for the change for models containing the predictor variables are given (Payne, 1987). The analysis employs a binominal error

Model	Constant	Size (W)	Photoperiod regime (PR)	Sex (S)	$W \times$ PR	$S \times$ PR	$W \times S$	$S \times W \times$ PR	Scaled deviance	G	P
0	−0.317								123.28		
1	−3.487***	3.478***							107.70	15.58	< 0.001
2	−2.394*	3.726***	−2.368*						99.67	8.03	< 0.005
3	−1.647	3.249***	−2.288*	−0.961					96.92	2.75	0.09
4	−0.553	1.020	−0.928	0.274	0.770	0.810			96.48	0.44	0.49
5	0.235	0.439	−1.656	−0.967	1.033		0.660		96.01	0.47	0.47
6	−0.310	0.753	−0.147	−0.662	0.628	−1.217	0.928		94.17	1.84	0.16
7	0.094	0.300	−1.125	−1.162	1.029	0.684	1.223	−1.034	92.08	2.09	0.18

Asterisk = coefficient/SE significant by Wald test (Hosmer and Lemeshow, 1989), $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$.

3.2. Growth in relation to photoperiod and sex

No fish died during the experiment. Males and females differed in growth pattern (Figs. 3 and 4; Table 1), with females being larger than males from early October 1992 onwards (Fig. 3, one-way ANOVA, $P < 0.01$). Further, the fish reared on the different photoperiod regimes differed in their growth patterns (Figs. 3 and 4). No initial (January 1992) size differences between the photoperiod groups were found within each sex (one-way ANOVA, $P > 0.5$, $1 - \beta > 0.7$, Fig. 3). Among females, the LD24:0 group had the lowest mean weight from late May 1992 to early February 1993, significant differences being recorded between May and August (Fig. 3A, one-way ANOVA, $P < 0.05$). Among the males, the fish exposed to LD24:0 were smaller from early July to early December, differences from other groups being significant in July and August (Fig. 3B, one-way ANOVA, $P < 0.05$). However, during the later stages of the experiment mean weights of the LD24:0 fish were higher than those of the LDN groups (Fig. 3, Table 1). Further, females from LD24:0 were significantly larger than females from LDN in June 1993 (Fig. 3A, one-way ANOVA, $F_{2,39} = 3.42$, $P < 0.05$). The LD16:8 group had higher, but not significantly higher, mean weights than LDN from December onwards among the females ($1 - \beta > 0.4$, Fig. 3A) and from February 1993 onwards for the males ($1 - \beta > 0.5$, Fig. 3B). Final mean weights of the fish in the LDN groups were lower than those of fish in the LD16:8 and LD24:0 groups (LDN: 1290 g, 909 g; LD16:8: 1727 g, 1075 g; LD24:0: 1777 g, 1055 g for females and males, respectively).

During the early stages (January 1992–July 1992) of the experiment growth rates were lower for both males and females in the LD24:0 than in the LDN and LD16:8 groups (Fig. 4), whereas during the later stages of the experiment fish in the LD24:0 group had the highest growth rates (Fig. 4). The GCM analyses revealed growth differences between photoperiod regimes for both sexes (Fig. 4). Individual growth

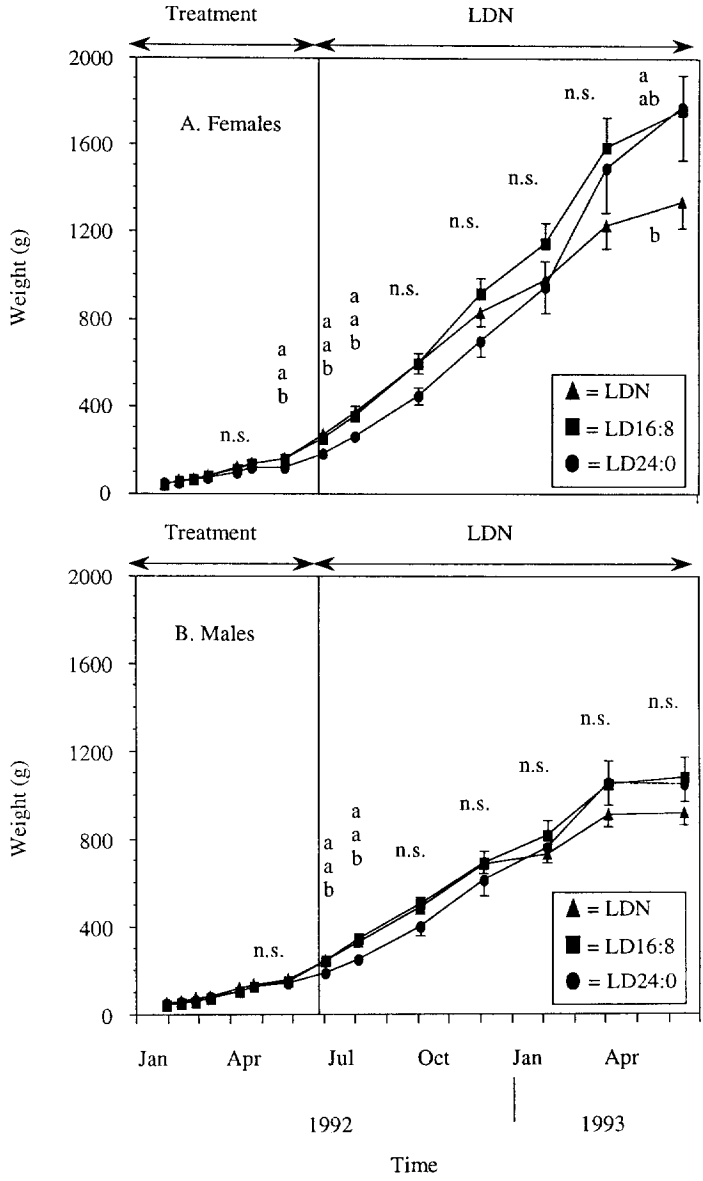

Fig. 3. Mean weight of turbot reared under three photoperiod regimes. Vertical line indicating SE may be obscured by symbol. Different letters indicate statistical differences ($P < 0.05$), with a indicating significantly higher mean weight compared to b. n.s. = not significant. A. females, B. males. Period with different photoperiods (Jan. 1992–May 1992) is marked with vertical line.

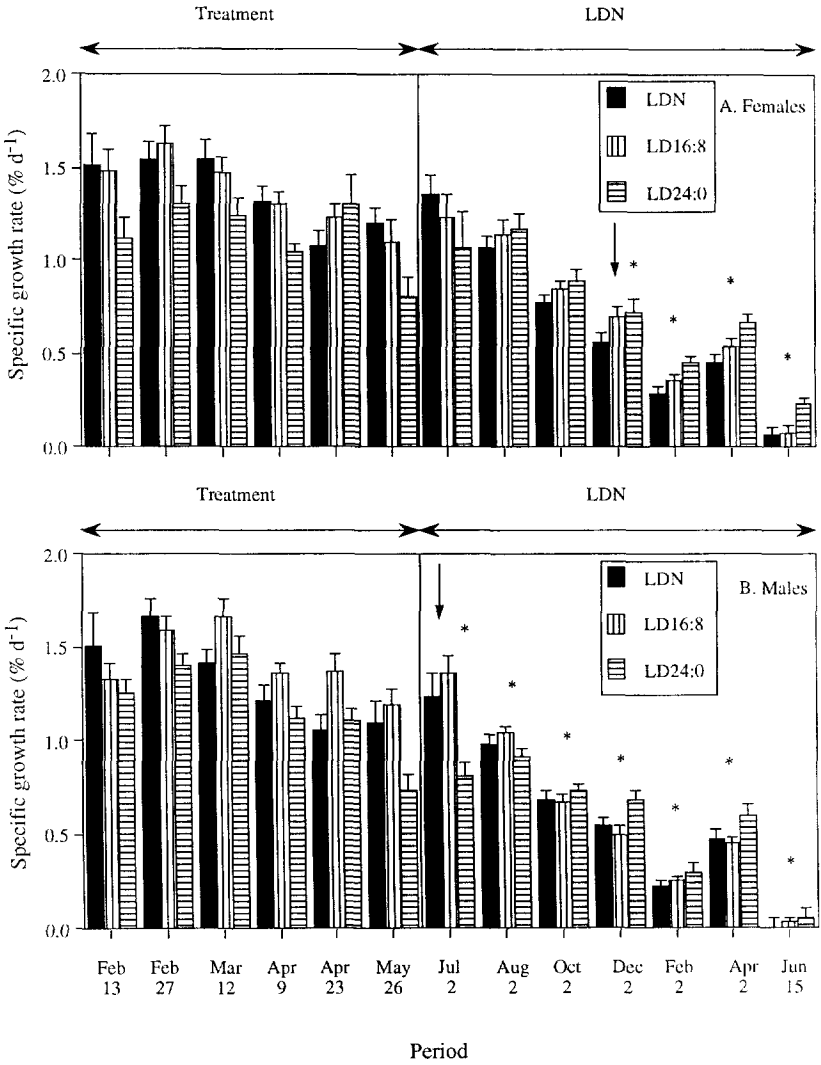

Fig. 4. Specific growth rates of individually tagged turbot reared under three photoperiod regimes. A. females, B. males. Arrows mark the first time period where groups differ in growth rate (GCM MANOVA). Asterisks indicate significant difference in growth. Period with different photoperiods (Jan. 1992–May 1992) is marked with vertical line. Data are shown as treatment means (SE).

trajectories in females exposed to the three photoperiods were different from early October 1992 onwards (Fig. 4A, $MANOVA_{(GROUP)}$, Wilk's lambda $(\Lambda)_{8,60} = 0.604$, $P < 0.05$). In males the growth trajectories of the photoperiod groups differed significantly from late May 1992 onwards (Fig. 4B, $MANOVA_{(GROUP)}$, Wilk's lambda $\Lambda_{14,62} = 0.604$, $P < 0.05$). The LD24:0 group had the highest average growth rate (0.5

and 0.6% d^{-1} for females and males, respectively) whereas fish in the LDN groups displayed the lowest average growth rate (0.3 and 0.5% d^{-1} for females and males, respectively). Growth rate was highest for all groups at the start of the experiment and decreased thereafter (Fig. 4).

3.3. Growth in relation to photoperiod and maturation

Growth of males was significantly influenced by maturation status and photoperiod treatment (Table 1). From October 1992 onwards the maturing males were larger than the immature males (two-way ANOVA, Table 1). For both maturing (M) and immature (IM) males of the LDN group the mean weights were lower compared with the corresponding fish on LD16:8 or LD24:0 (LD16:8-M, LD16:8-IM, LD24:0-M and LD24:0-IM) from April 1993 onwards (two-way ANOVAs, Table 1). Growth of females was influenced by maturation status from February 1993 onwards (two-way ANOVA, Table 1). During this period the maturing females in the LD16:8 and the LD24:0 group had higher mean weights than the maturing females on LDN (Table 1). Females on LD24:0 (M and IM) had lower mean weights than corresponding fish on LDN from July

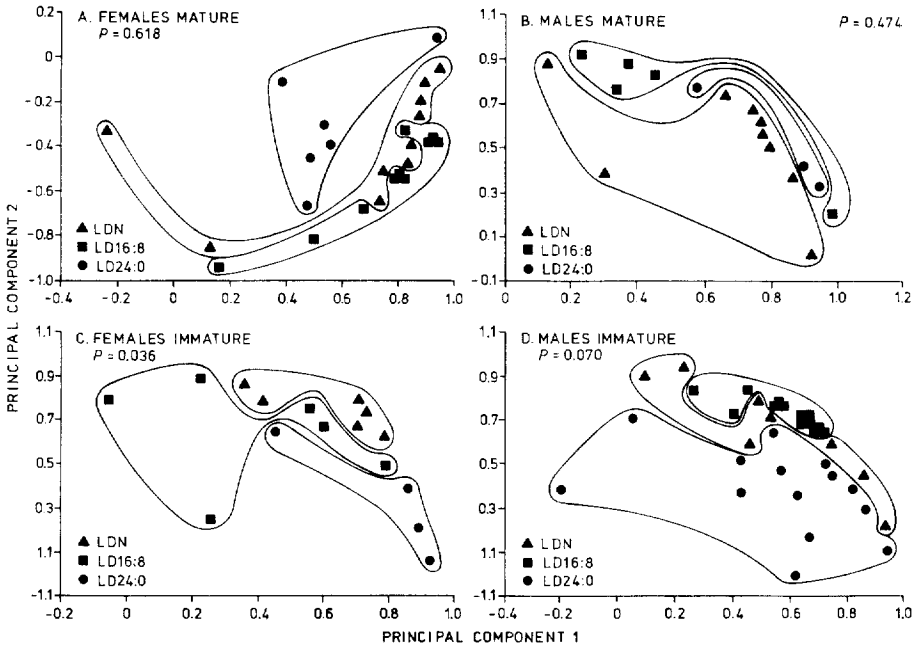

Fig. 5. Principal component plots for the factor loadings of the two-factor solution of the matrix of all growth rates and size rankings of each individual from January 1992 to June 1993. A. mature females, B. mature males, C. not mature females, D. not mature males. To improve the readability range areas were drawn for each photoperiod regime. P value for Wilk's Λ is included in the figure. Statistical results of the two-factor solution are given in Table 3.

Table 3
One-way MANOVA for principal component factor scores on growth rates and weight ranking of 94 tagged fish throughout the experiment

Grouping	n	Mean factor scores		P for Wilk's Λ	Variance explained (cumulative %)	
		Factor 1	Factor 2		Factor 1	Factor 2
A. Females, mature						
				0.618	73.4	84.8
LDN	10	0.823	0.014			
LD16:8	10	0.890	0.003			
LD24:0	6	0.808	−0.169			
B. Males, mature						
				0.474	79.3	92.2
LDN	9	0.874	−0.069			
LD16:8	5	0.866	0.236			
LD24:0	3	0.944	−0.155			
C. Females, immature						
				0.036	74.8	85.5
LDN	6	0.938	0.038			
LD16:8	6	0.801	0.200			
LD24:0	4	0.806	−0.309			
D. Males, immature						
				0.070	76.9	85.6
LDN	7	0.890	−0.017			
LD16:8	14	0.915	0.082			
LD24:0	14	0.810	−0.054			

Separate tests were performed for different experimental groups and for mature females (A), mature males (B), immature females (C) and immature males (D).
The significant probability (P) for the Wilk's lambda (Λ), and cumulative percent of variance explained by the factor loadings is also shown.
n = number of fish in each category.

to October 1992 (Student–Newman–Keuls test, Table 1) and although not significant the opposite result was seen from December onwards (M) and in June 1993 (IM; Table 1).

The principal component analyses indicated that the size ranking and growth pattern differed between the photoperiod groups (Fig. 5C, D). Further, the result of one-way MANOVA for the factor loadings showed that the differences in growth between the photoperiod groups were due to different growth patterns of the immature fish (Table 3; Fig. 5C, D). Size ranking and growth pattern were significantly different between the photoperiod groups in immature females (Wilk's $\Lambda_{4,24} = 0.44$, $P = 0.036$, Fig. 5C, Table 3), and tended towards significance in immature males (Wilk's $\Lambda_{4,62} = 0.76$, $P = 0.070$, Fig. 5D, Table 3). No differences were found for the mature fish (Table 3, $P > 0.45$, $1 - \beta > 0.6$). The factor analyses explained between 84 and 92% of the variance in the data (Table 3).

4. Discussion

This study demonstrates a significant long-term effect of photoperiod on growth and age at first maturity in turbot. There were no initial differences in mean weights between maturing and immature fish within each sex, within each photoperiod treatment. However, in the latter stages of the experiment, fish in the groups exposed to extended photoperiod during the first winter tended to be larger than controls, irrespective of sex and maturational status (Table 1).

Overall growth differences among males between photoperiod groups could have been the result of the lower proportion of maturing fish in the LD16:8 and LD24:0 groups matured. Earlier studies have shown that male flatfish grow slowly after reaching maturity (Jones, 1974; Druzhinin and Petrova, 1980; Jákupsstovu and Haug, 1988; Miller et al., 1991; Imsland et al., 1997). In females however, no differences in proportions of maturing fish were seen amongst fish exposed to the different photoperiods, so growth differences could not be explained as a result of maturational differences. Further, the results of the factor analyses showed that size ranking and growth pattern of immature fish differed between the photoperiod groups for both sexes. Accordingly, growth differences may be explained on the basis of different growth patterns amongst immature fish in the different photoperiod groups, indicating a long term growth-promoting effect of long day (LD16:8) and continuous light (LD24:0). A growth promoting effect of extended daylength and continuous light is well documented for salmonids in fresh water (Clarke et al., 1981; Stefansson et al., 1991; Berg et al., 1992) and postsmolts in sea water (Saunders and Harmon, 1988; Kråkenes et al., 1991; Taranger, 1993). In contrast, earlier studies on marine species have revealed only small effects of extended photoperiod on growth compared with those observed for anadromous species (sole, *Solea solea*, Fuchs, 1978; plaice, *Pleuronectes platessa*, and sole, Fonds, 1979; splitnose rockfish, *Sebastes diploproa*, Boehlert, 1981; Atlantic cod, *Gadus morhua*, Folkvord and Otterå, 1993; Atlantic halibut, *Hippoglossus hippoglossus*, Hallaråker et al., 1995; turbot, Imsland et al., 1995, Person-Le Ruyet, IFREMER, Brest, unpublished results). The large growth promoting effect of LD16:8 and LD24:0 in the present study is, therefore, in contrast with most earlier findings on marine species. The results from the present study demonstrate that exposure to extended photoperiods during the first winter may alter the long-term growth pattern of both maturing and immature fish resulting in increased overall growth.

The higher proportion of males which matured under LDN than under LD16:8 and LD24:0 (56.0% vs. 24.3% and 17.4%, respectively), indicates that there is phenotypic plasticity in the onset of puberty in turbot. Thus, environmental manipulations carried out on juvenile males can affect the age of first maturation even though fish may be exposed to common environmental signals at a later stage. In contrast, there were no differences in the proportion of maturing females among the different photoperiod groups. The process of maturation in fish is energetically expensive, especially for females, and females of many flatfish species mature at an older age than do males (Bowering, 1976; Druzhinin and Petrova, 1980; Jákupsstovu and Haug, 1988; Armstrong and Starr, 1994). Further, histological data on flatfishes indicate that the process of maturation may span over a period of 2–3 yr (Jones, 1974; Burton and Idler, 1984;

Déniel, 1984; Rijnsdorp, 1989). In captivity turbot usually mature at an age of 2–3 yr (Devauchelle et al., 1988; Imsland et al., 1997), and growth differences between early and late maturing fish can be detected from nine months post-hatch in both sexes (Imsland et al., 1997). The differences in proportions of maturing fish between males and females seen in the present study indicate that the decision to mature is taken at an earlier stage in turbot males than in turbot females, and that exposure to extended photoperiods during the first winter may affect the age at first maturity in males to a larger extent than females. This is supported by our findings that exposure to extended photoperiods during the first winter reduced the proportion of maturing males in those groups (Fig. 2) whereas this early treatment did not effect the females. Earlier studies on turbot have indicated that males start their maturation process at an earlier age than females (Jones, 1974; Devauchelle et al., 1988; Imsland et al., 1997). Further, Fores et al. (1990) studied the effect of sudden change in light regime (from constant 8-h light to constant 16-h light) on maturity of turbot, and found that the fish responded positively but the males showed a faster response than the females.

Recent studies have shown that the incidence of maturation in Atlantic salmon can be reduced by rearing the fish under constant light during winter and early spring (Hansen et al., 1992; Taranger, 1993), and that the annual cycle of gonadal growth may start in the autumn up to a year before first maturation (e.g. Thorpe, 1994). Scott and Sumpter (1983) showed that the physiological decision about whether or not to finalize the maturation process in rainbow trout (*Oncorhynchus mykiss*) in a given year was taken under conditions of increasing daylength (spring). It has been suggested (Hansen et al., 1992; Taranger, 1993) that constant light in winter and early spring may advance the timing of the decision of whether to continue the maturation process to a time of year when growth rate and/or energy status are low. If the fish 'turn off' the maturation process, more energy may be channelled into somatic growth compared to maturing fish (Stearns, 1992). It is possible that a similar mechanism might explain the growth enhancement seen in the LD24:0 and LD16:8 fish in the later stages (second winter) of the present study. Few studies address the effect of photoperiod on growth and age at first maturation in marine species. Recent studies on Atlantic cod show that rearing fish under constant light has a growth promoting effect and reduces the incidence of maturation (Hansen et al., 1995; G. Nyhammer, Department of Fisheries and Marine Biology, N-5020 Bergen, Norway, pers. comm.). The findings of the present study are in line with these preliminary results on marine species as well as with the results on salmonids (Hansen et al., 1992; Taranger, 1993).

Large differences in growth between maturing and immature fish were noted in the present study, in line with findings those of Rijnsdorp (1993) and Imsland et al. (1997). The increased growth of the maturing fish seemed to occur before endocrine changes associated with sexual maturation in turbot would be expected (Grung et al., 1996). Thus, it is suggested that the higher growth in maturing turbot may act as a stimulus to sexual maturation. This may be reflected by the findings of the present study where maturity was size dependent (Table 2) so that the faster growing fish within each photoperiod regime matured earlier than slower growing ones. Some recent studies on flatfish have also indicated that maturity is size depended (plaice, Rijnsdorp, 1993; turbot, Imsland et al., 1997). It is generally assumed that fish mature when they have

passed a size or age threshold (Alm, 1959; Roff, 1982; Stearns, 1992), and following maturation, there is a positive relationship between fecundity and body size in females (Wootton, 1979). Burton (1994) highlighted the importance of nutritional status in governing gametogenesis in females: non-reproductive fish were likely to result if feeding was restricted prior to, and immediately subsequent to, spawning and it was concluded that this period constitutes a nutritionally sensitive critical period. In the present study all fish were fed in excess throughout the experiment, reducing the possibility of poor nutritional status being a factor influencing maturation although this possibility can not be excluded.

Females grew better than males in the present study in accordance with earlier studies on turbot (Jones, 1974; Devauchelle et al., 1988; Déniel, 1990), and other flatfish species (Druzhinin and Petrova, 1980; Jákupsstovu and Haug, 1988; Miller et al., 1991). These differences may be related to the higher incidence of maturation in females in the study as maturing females are reported to grow better than immature males in flatfishes (plaice, Rijnsdorp, 1989, 1993; turbot, Imsland et al., 1997). Another possible explanation for the growth divergence between sexes may be differences in food intake and digestive tract size of females and males as shown for the dab, *Limanda limanda* L. (Lozán, 1992).

Replicate tanks were used when the fish were reared under different photoperiods (December 1991–May 1992). However, in the latter stages of the experiment when the fish were exposed to the same photoperiod (LDN) the fish were reared together in one tank. This could mean that part of the effects of photoperiod on growth and maturation might be explained by a tank effect. However, earlier studies on the juvenile stages of the same fish material revealed only marginal tank effects (Sunde, 1993; Imsland et al., 1995, 1996) on growth. Rearing the fish together in the same tank would also mean that all the fish were exposed to the same tank effect.

In conclusion, the results of the present study indicate that extended daylength and continuous light during the first winter has a significant effect on subsequent growth and age at first maturity. The growth enhancing effect of the LD16:8 and LD24:0 photoperiods was related to influences that these extended photoperiods had on the growth patterns of the immature fish. Moreover, fewer males matured in the LD16:8 and LD24:0 groups than in the LDN group. This may have practical value because male turbot grow little after reaching maturity.

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