GROWTH, OXYGEN CONSUMPTION AND ACTIVITY OF JUVENILE TURBOT (*SCOPHTHALMUS MAXIMUS* L.) REARED UNDER DIFFERENT TEMPERATURES AND PHOTOPERIODS

ALBERT K. IMSLAND, A. FOLKVORD and S.O. STEFANSSON

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

ABSTRACT

Juvenile turbot (5-125 g) were reared under two experimental temperatures: 10°C and 16°C, and three experimental photoperiods: LDN (natural photoperiod), LD16:8 (16 h light: 8 h darkness), LD24:0 (continuous light), to study effects of temperature and photoperiod on growth, activity and oxygen consumption. Growth was strongly affected by temperature and was higher at 16°C than at 10°C. Continuous light had a growth-promoting effect at 10°C from mid-December to late March, while at 16°C this effect was restricted to December and January. A seasonal change in the condition index was found. The groups reared in continuous light had higher condition indices in winter. The experimental groups held at 16°C had a higher O_2 consumption than those at 10°C. The LD24:0 groups invariably had a higher overall O_2 consumption than did the LDN and LD16:8 groups, the differences being caused by reduced O_2 consumption in the latter groups during darkness. The LD24:0 groups displayed higher activity than the LDN groups, in which activity was very low at night.

Key words: growth, oxygen consumption, activity, photoperiod manipulation, turbot, *Scophthalmus maximus*

1. INTRODUCTION

Experiments to cultivate turbot have been going on for more than a century (Holt, 1892; Malard, 1899; Anthony, 1910), and techniques for large-scale rearing of turbot fry were developed in Europe during the 1970s and 1980s (Jones, 1972; Bromley, 1979; Howell, 1979; Bromley & Sykes, 1985). Growth studies have focused on all stages from metamorphosis to market size, with temperature being the main factor investigated (Purdom *et al.*, 1972; Jones *et al.*, 1981; Person-Le Ruyet *et al.*, 1981; Iglesias *et al.*, 1987). Smith (1976) has demonstrated that a relatively high growth rate may be obtained over the temperature range from 10 to 18°C. However, more detailed studies have shown that a higher growth rate can be obtained at 16°C than at 10°C (Jones *et al.*, 1981; Person-Le Ruyet *et al.*, 1981; Iglesias *et al.*, 1987). Information concerning the effects of other environmental factors, *e.g.* photoperiod, on growth of juvenile turbot is scarce. When studying the ecology of wild turbot, Jones (1973) found that growth of juvenile turbot showed a distinct seasonal pattern: higher in summer than in winter. He suggested that this growth pattern was partly due to seasonal changes in day length.

Extended photoperiod (*i.e.* beyond the natural day length) has been shown to lead to increased growth rate of several fish species, *e.g.* Atlantic salmon, *Salmo salar*, juveniles in freshwater (Saunders *et al.*, 1989; Stefansson *et al.*, 1989; Berg *et al.*, 1992) and postsmolts in seawater (Saunders & Harmon, 1988; Kråkenes *et al.*, 1991). Corroborative evidence for the growth-promoting effect of extended photoperiod has been demonstrated in studies with green sunfish, *Lepomis cyanellus* (Gross *et al.*, 1965), channel catfish, *Ictalurus punctatus* (Kilambi *et al.*, 1970), plaice, *Pleuronectes platessa*, and sole, *Solea solea*, (Fonds, 1979), juvenile splitnose rockfish, *Sebastes diploproa* (Boehlert, 1981) and Atlantic cod, *Gadus morhua*, (Folkvord & Otterå, 1993).

The following experiment was designed to investigate the effect of temperature and photoperiod and their interaction on growth of juvenile turbot. Based on the knowledge of the life history of turbot and earlier experiments on this and other species, two tempera-

tures (10°C and 16°C) and three light regimes (natural photoperiod, LDN, 16 h light and 8 h darkness, LD16:8, and constant light, LD24:0) were chosen. In addition, activity and oxygen consumption were measured to study how these variables were influenced by temperature and photoperiod, as well as their interaction with growth rate.

2. MATERIALS AND METHODS

2.1. FISH STOCK AND REARING CONDITIONS

Eggs from one female turbot and sperm from two males were pooled and incubated on 7 July 1991. After hatching the larvae were transferred to plastic bags (Berg et al., 1985) floating in a 53000 m³ seawater basin at Selvåg (just south of Bergen), with a rearing temperature of ~18°C. From 16 July the larvae were fed natural zooplankton filtered from the basin. After metamorphosis the juveniles were transferred to rearing tanks (1 m³) with a temperature of 13 to 16°C and fed a commercial dry diet. In October the juveniles were brought to the Industrial Laboratory (ILAB) at the Bergen High Technology Centre (BHTC) and reared at 13°C. The fish were reared under the natural light regime of Bergen (60°25'N, 5°20'E), from first feeding until the start of the experiment. The experimental fish used came from a group of 2800 juvenile turbot of which 1200 were used in this study. At the start of the experiment the fish had a mean weight of 7.1 g (s.d. = 1.7 g).

The studies were carried out from 7 November 1991 to 23 April 1992. The experimental tanks were square, grey, covered fibreglass 1m² tanks with a rearing volume of 400 dm³. Seawater with a salinity of S=34.5±0.2 was pumped from 90 m depth. Water flow was initially set at 20 dm³·min⁻¹ for all experimental tanks. The oxygen concentration was always kept above 6.5 mg O_2·dm³. Light was provided by one 36 W fluorescent daylight tube installed in the tank cover and photoirradiance at the tank bottom was approximately 4.24 µE·m⁻²·s⁻¹. A computer program (Lysstyr 2.00; Hansen, 1990) generated a simulated natural light regime including twilight periods.

2.2. EXPERIMENTAL DESIGN

On 7 November the fish were weighed and randomly distributed over 12 tanks (100 in each tank). The fish were transferred from the holding temperature of 13°C directly to the two experimental temperatures of 10°C and 16°C. Temperatures remained within ±0.2°C of that prescribed throughout the experimental period. On 4 December, three light regimes were established for groups of fish held on each temperature regime, making a total of six experimental groups all consisting of two replicate tanks. One group under each thermal regime remained on natural photoperiod of Bergen, LDN (~7 h light in mid-December, ~16

h light in mid-April). The two other experimental photoperiods were 16 h light : 8 h darkness, LD16:8 (04.00 - 20.00), and constant light, LD24:0. Commercial dry diet for flatfish (Flatfiskfôr, Felleskjøpet A/S, sizes 1.8, 3.0 and 4.0 mm pellets) was dispensed in excess from automatic feeders every 4 min during the natural photophase.

All fish were weighed individually to the nearest 0.01 g every 2 weeks during the experiment, except during the period from 21 November to 4 January when the fish were weighed every 3 weeks. Along with weighing, 20 fish were randomly chosen from each group and their standard length (SL) recorded to the nearest mm. Specific growth rate (SGR) was calculated according to the formula of Houde & Schekter (1981).

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

where $g = (\ln(W_2) - \ln(W_1)) (t_2 - t_1)^{-1}$ and W_2 and W_1 are mean weights at days t_2 and t_1, respectively. SGR 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) were not included in the analysis. The SL and corresponding weight measurements were used to obtain a log weight - log length regression for each temperature. The regression coefficient (β) was tested for homogeneity using analysis of covariance (ANCOVA). Provided homogeneity was documented, pooling of the data was performed in order to calculate common β-value to be used in calculation of the condition index (K). The condition index was defined as:

$$K = 100 \cdot W \cdot L^{-\beta}$$

where W is the weight of the fish (g) and L the corresponding standard length (mm).

Open respirometry experiments were conducted in the rearing tanks for all six groups on 25-26 March, 8-9 April and 22-23 April. O_2 measurements in inlet and outlet water were carried out every hour during the 24-hour cycle and the fish were weighed immediately afterwards. The fish were fed during the respirometry experiments. 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.

The specific O_2 consumption rate ($\dot{V}O_2$, mg·kg⁻¹·h⁻¹) was calculated according to the formula:

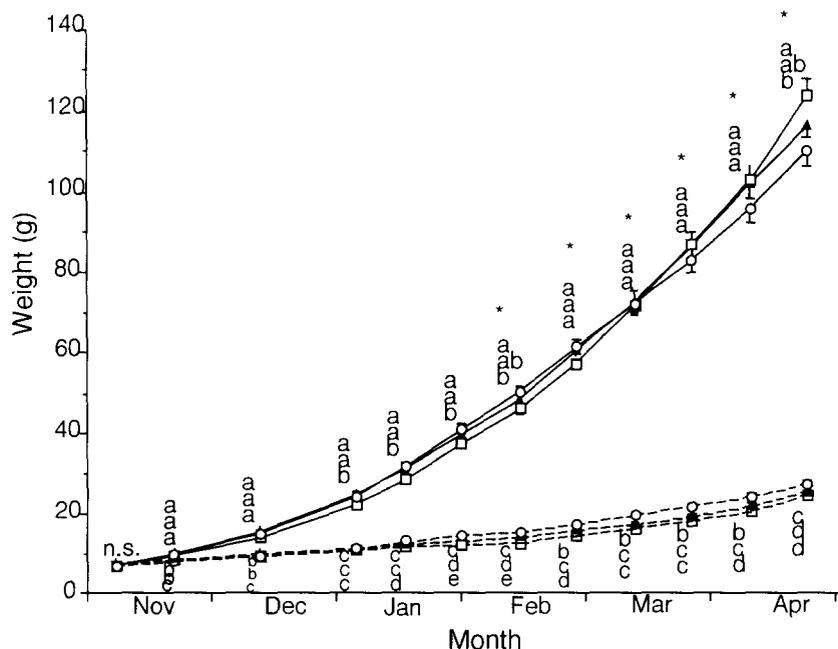$$\dot{V}O_2 = (\dot{V}_F \cdot \delta pO_2) (B)^{-1}$$

Fig. 1. Mean weight of juvenile turbot under two temperatures and three photoperiods. Different letters indicate statistical differences with a as the highest value, ▲=LDN, ☐=LD16:8,○= LD24:0. Broken lines = 10°C, solid lines = 16°C, n.s. = not significant. * indicates significant interaction between photoperiod and temperature.

(Jobling, 1982; Brix, 1992), where $\dot{V}_F$ is the water flow ($dm^3 \cdot h^{-1}$), through the tank, δpO_2 the difference in O_2 concentration between the inlet and outlet water, and B is the total biomass in the tank. As the biomass of the 10°C groups was lower than of the 16°C groups, water flow was reduced in the 10°C groups to 12 $dm^3 \cdot min^{-1}$ in order to conduct accurate measurements of the oxygen concentration in the outlet water. The water flow at 16°C was kept at 20 $dm^3 \cdot min^{-1}$. When analysing the oxygen data we combined three adjacent measurements based on a visual interpretation of the different phases in O_2 consumption during the 24-hour cycle. The hour of first light (dawn) in the LDN groups was used as the starting point for combining the measurements.

Activity observations were carried out in March and April 1992. Observations lasted 15 min and were video-taped for subsequent analysis. Four groups (tanks) were studied: LDN-10°C, LD24:0-10°C, LDN-16°C and LD24:0-16°C. The LD16:8 groups could not be included for practical reasons. Observations were performed when feeding commenced (morning), at noon, and when feeding was terminated (evening); additional observations were made at: 22.00, 24.00, 02.00, 04.00 Central European Time (CET), and when feeding commenced the following morning. An infrared light source and an underwater camera were used to observe the fish at night in the LDN groups. In

order to quantify the activity, every movement was recorded and counted. Movement was defined as every event that involved either vertical or horizontal movement of the whole fish. Of the 15 min filmed, three randomly chosen 2-min subsamples were analysed. During feeding hours, filming began at the start of each feeding pulse. The number of movements counted in each subsample was divided by the total number of fish in the tank and by duration of the period (min), to give activity frequency as movements $\cdot fish^{-1} \cdot min^{-1}$.

2.3. STATISTICAL ANALYSIS

To assess for normality of distributions a Kolmogorov-Smirnov test (Zar, 1984) was used. The homogeneity of variances was tested using the Levene F test (Brown & Forsythe, 1974). Three-way nested Model III ANOVA (Scheffé, 1959), where the replicates were nested within temperature and photoperiod groups, was applied to calculate the effect of photoperiod and temperature on weight, condition index, oxygen consumption and activity at respective time periods. The growth rates of the different photoperiod groups were tested in a one-way Model I ANOVA. Significant ANOVAs were followed by a Student-Newman-Keuls multiple comparison test to determine differences among experimental groups.
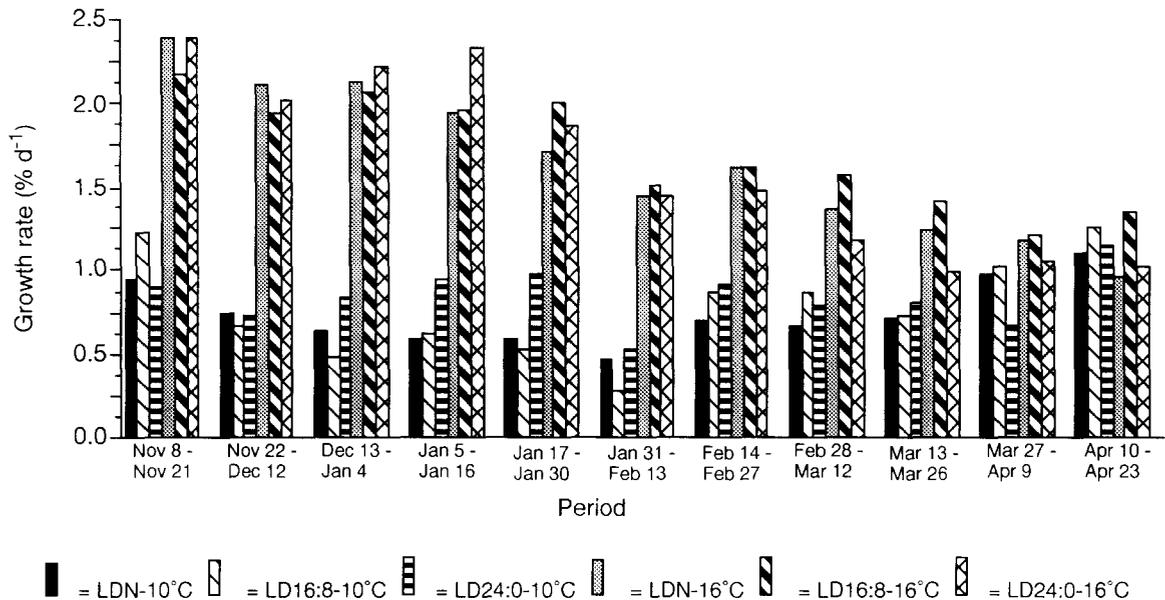
Fig. 2. Growth rate of juvenile turbot under two temperatures and three photoperiods.

The SGR and GM linear regressions were analysed using a covariance analysis (Sokal & Rohlf, 1981). Data on mortality were tested in a chi-square test (Zar, 1984). If not otherwise stated, a significance level of 0.05 was used.

3. RESULTS

3.1. MORTALITY

In December a bacterial infection, *Aeromonas* sp. (Roberts, 1993) was detected in the fish (O.M. Rød-seth, Institute of Marine Research, Bergen, pers. comm.). Oral antibiotica, *Flumequine*; 30 mg·kg^{-1}·d^{-1}, treatment was given from 13 December to 18 Decem-

ber. An average mortality of 11.6% was recorded. The mortality was higher at 10°C (17.2%) than at 16°C (6.0%). Total treatment mortality was significantly higher at 10°C than at 16°C (χ^2 = 44.89, p < 0.01). Mortality varied among photoperiod groups and was significantly higher in the LD16:8 groups at both temperatures than in the LDN groups (χ^2= 11.15, p < 0.01, χ^2 = 16.67, p < 0.01). No differences were found in mortality of the LDN and LD24:0 groups at both temperatures. A size-dependent mortality was found as the dead fish were significantly smaller than the surviving fish (*t*-test) in the LD16:8 groups at 16°C, and in all groups at 10°C.

3.2. GROWTH

Mean weights were higher at 16°C than at 10°C from late November onwards (three-way nested ANOVAs, p < 0.01, Fig. 1). At 10°C the LD24:0 group had higher mean weight than LDN from early February onwards. At 16°C the mean weight of LDN and LD24:0 was higher than that of LD16:8 from early December to mid-February. The LD16:8-16°C had the highest final mean weight in late April. However, a size-dependent mortality was found in this group which could have led to higher mean weight than found in the other groups at 16°C. Significant interactions (three way nested ANOVAs, Fig. 1) between the effects of photoperiod and temperature on mean weights were found from mid-February onwards.

At 10°C the fish on LDN showed a growth pattern (Fig. 2) where growth rate changed according to

TABLE 1
Results from growth rate - geometric mean weight regression of juvenile turbot at two temperatures and three photoperiods. The regression equation is given as $Y_i = \alpha + \beta X_i$·α is the regression constant, β is the regression coefficient, and R^2 is the coefficient of correlation. In the regression, H_0: β = 0; thus rejection (p < 0.05) means that growth of the fish varies with size.

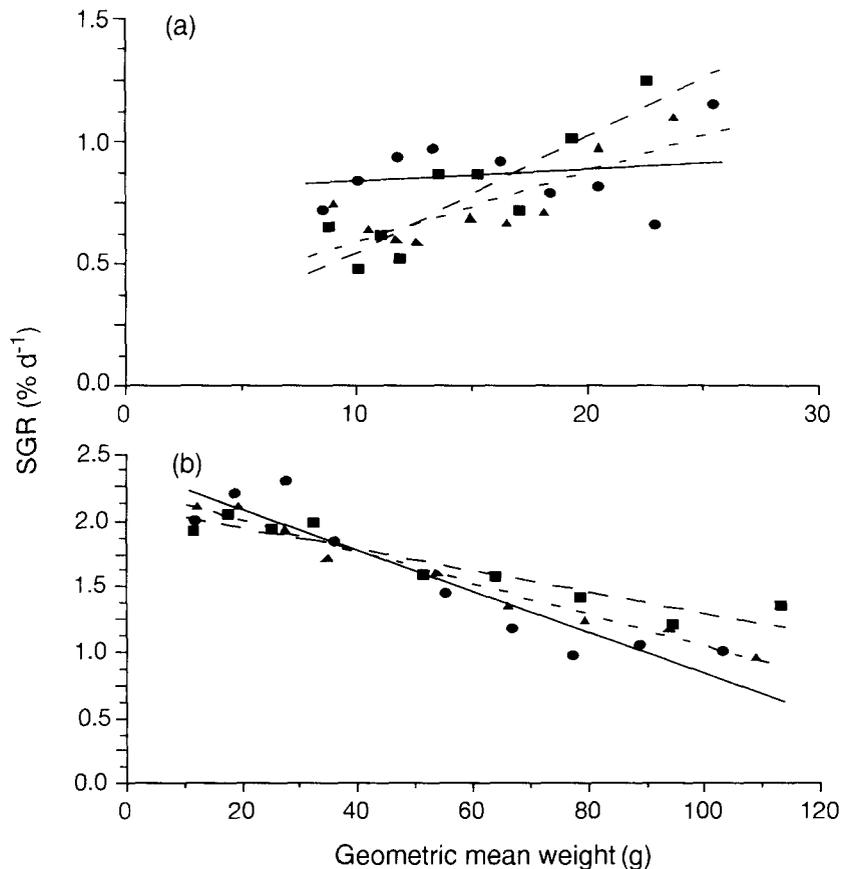|	n	b	p (β)	a	p (α)	R^2
LD24:0-16°C	9	-0.015	< 0.001	2.398	< 0.001	0.87
LD16:8-16°C	9	-0.008	< 0.001	2.118	< 0.001	0.88
LDN-16°C	9	-0.012	< 0.001	2.237	< 0.001	0.97
LD24:0-10°C	9	0.005	0.593	0.783	0.002	0.04
LD16:8-10°C	9	0.047	0.014	0.086	0.562	0.78
LDN-10°C	9	0.028	0.009	0.304	0.051	0.64

Fig. 3. Growth rate-geometric mean regression of juvenile turbot at 10°C (a) and 16°C (b). Symbols: - - - and ▲= LDN, —— and ■=LD16:8, —— and ●= LD24:0. The regression equations are given in Table 1. Replicates are combined. The growth rates during acclimation are not included in the analysis.

changes in day length, reaching a low in January and increasing throughout the study. In contrast, at 16°C growth rate of the LDN group was highest in November and decreasing throughout the experimental period.

Under both thermal regimes the growth pattern of LD24:0 groups differed from that of the LDN groups (Figs 2 and 3). At 10°C the LD24:0 groups had a higher growth rate than LDN groups between mid-December and late March. In this period the LD24:0 groups displayed a significantly higher growth rate than the other groups at 10°C (one-way ANOVA, $F_{2\ 18}$ = 3.90, p = 0.038). At 16°C the LD24:0 groups had a higher growth rate than LDN groups from mid-December to late January. Growth rate at 10°C and 16°C showed a different pattern and was highly significant (ANCOVA, $F_{2\ 48}$ = 278.29, p < 0.001, Fig. 3).

The size specific growth rate differed between the two temperatures. Growth rate at 10°C increased with increasing weight in the LDN and LD16:8 groups (Fig.

3a, Table 1). The LD24:0 groups showed a different growth pattern, displaying only a weak correlation between growth and weight (R^2 = 0.04, Table 1). At 16°C all groups showed a decline in their growth rate with increasing weight (linear regression, p < 0.005, Fig. 3b, Table 1).

3.3. CONDITION INDEX

The regression coefficients were not significantly different (ANCOVA, $F_{1\ 1376}$ = 1.28, p > 0.5) so a common β-value could be used to calculate the condition index. The common β-value was 2.87, which gave the condition index (K):

$$K = 100W \cdot L^{-2.87}$$

The condition index declined in all groups from early November until mid-January (Fig. 4). Between mid-January and late March the condition index was
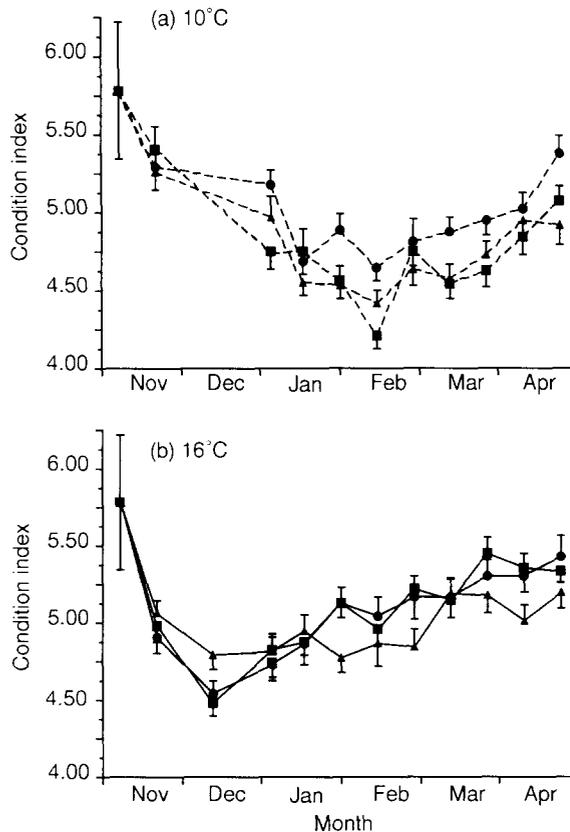
Fig. 4. Condition index of juvenile turbot reared under two temperatures and three photoperiods. ▲=LDN, ■=LD16:8, ●= LD24:0. a. Broken lines = 10°C, b. solid lines = 16°C. Due to disease in the fish, length was not measured at 10°C in December.

higher at 16°C than at 10°C. The condition index of the 10°C groups increased from mid-February onwards. In April there were no longer significant differences among the experimental groups.

At both temperatures the LD24:0 groups had generally a higher condition index than the LDN groups (Fig. 4). At 16°C both the LD24:0 and LD16:8 groups displayed generally higher K than LDN.

3.4. OXYGEN CONSUMPTION

At both temperatures the LDN groups showed a clear diurnal rhythm in their O_2 consumption (Fig. 5) with an increase in O_2 consumption in the morning following commencement of feeding and a decline in O_2 consumption in the afternoon. The LD16:8 groups showed a diurnal rhythm in O_2 consumption similar to that of the LDN groups.

The LD24:0 groups showed a different diurnal rhythm in O_2 consumption (Fig. 5). At night the

LD24:0 groups on both thermal regimes had higher O_2 consumption than the respective LDN and LD16:8 groups (three-way nested ANOVAs, p < 0.005). From late morning until late afternoon (10.00-18.00) O_2 consumption peaked and plateaued, with only slight differences among the different treatment groups within thermal regimes. As feeding ceased in late afternoon the O_2 consumption declined in all groups, the changes being less pronounced in the LD24:0 group than in the LDN and LD16:8 groups.

3.5. ACTIVITY

The overall activity was lower at 10°C than at 16°C (Fig. 6). At night the activity of the LDN groups was low, and it was generally lower for LD24:0-10°C than for LD24:0-16°C. All groups showed a distinct diurnal activity pattern, with greatest activity in the morning at commencement of feeding (Fig. 6) followed by a gradual decline until late afternoon. Activity declined rapidly in the afternoon in the LDN groups and was very low at night (Fig. 6). From late afternoon and at night the activity remained stable or decreased only slightly in the LD24:0 groups. The nocturnal activity of the LD24:0 groups was always significantly higher (three-way nested ANOVAs, p < 0.005) than in the LDN groups. At the commencement of feeding the LD24:0 groups were always more active (three-way nested ANOVAs, p < 0.01) than the LDN groups.

4. DISCUSSION

Growth rate of juvenile turbot was influenced by temperature, fish size and photoperiod. From the beginning of the study until April, the 16°C groups had a higher growth rate than those at 10°C. This is in accordance with earlier studies on this species (Jones et al., 1981; Heap & Thorpe, 1987). Further, size-dependent growth was significantly influenced by temperature. At 10°C there was an inverse relation between the slopes of the size versus growth rate regressions, with significant positive slopes in the LDN and LD16:8 groups. At 16°C, however, all regressions were negative. The increase in growth rate with increasing size seen at 10°C indicates that the optimum temperature for growth shifted downwards as the fish grew larger, in accordance with findings of Heap & Thorpe (1987) and Iglesias et al. (1987) on turbot, as well as the general pattern suggested by Brett (1979). At 16°C, which is near the optimum temperature for growth of juvenile turbot (Jones et al., 1981), the overall negative correlations between fish size and growth rate are in accordance with findings on various other fish species (see review by Brett, 1979). The relation between body size, temperature and growth seen in this study, and the shift to lower optimum temperature for growth with increasing size observed at 10°C may have important ecological implications. It could, for instance, help to
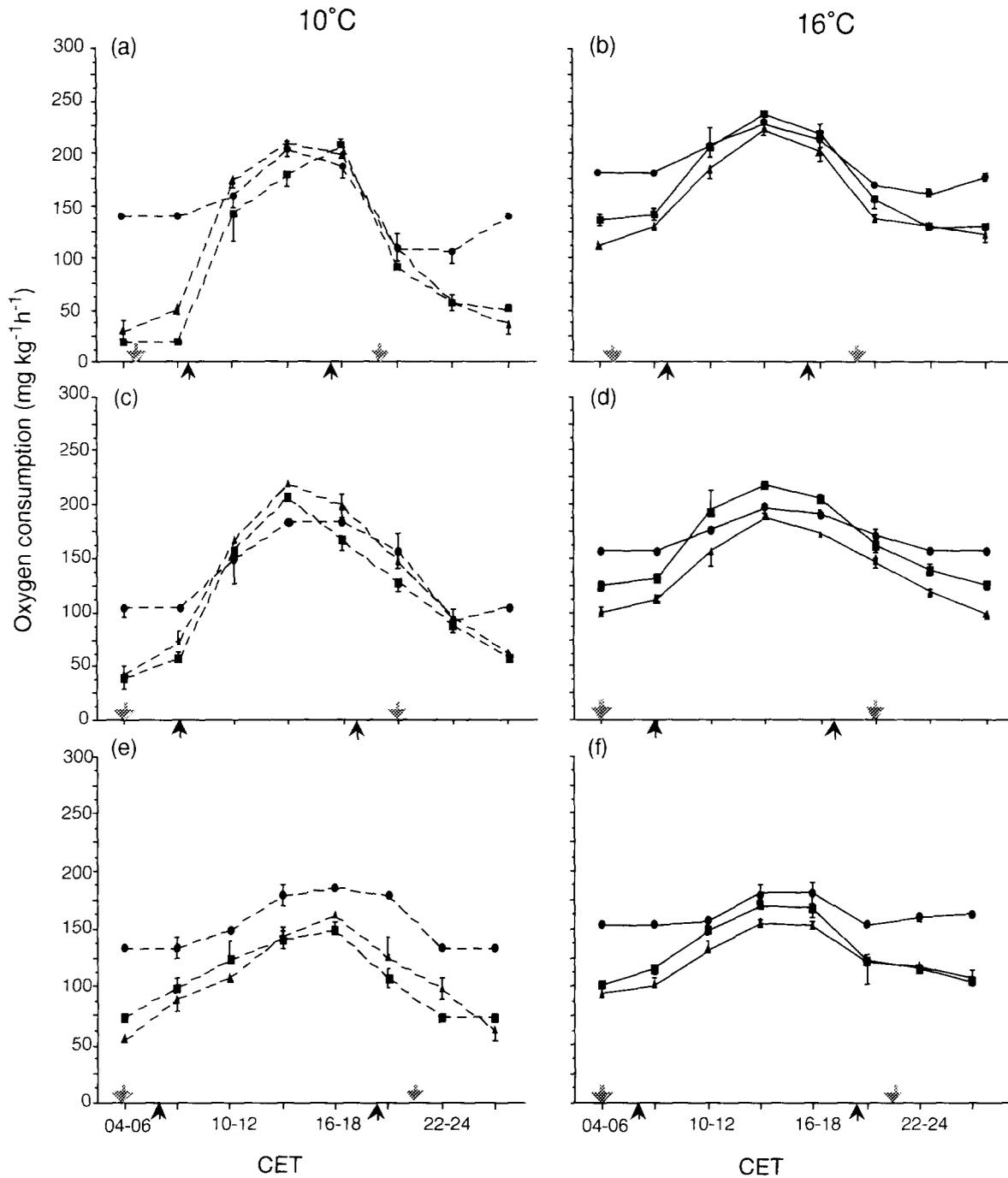
Fig. 5. Diurnal patterns in O_2 consumption of juvenile turbot under two temperatures and three photoperiods. a-b. 25-26 March; c-d. 8-9 April; e-f. 22-23 April. Symbols: ▲=LDN; ■=LD16:8, ●=LD24:0. Broken lines=10°C, solid lines=16°C. CET = Central European Time. Arrows beneath line (filled) mark feeding regime, arrows above line (shaded) mark light on/light off for LDN groups.
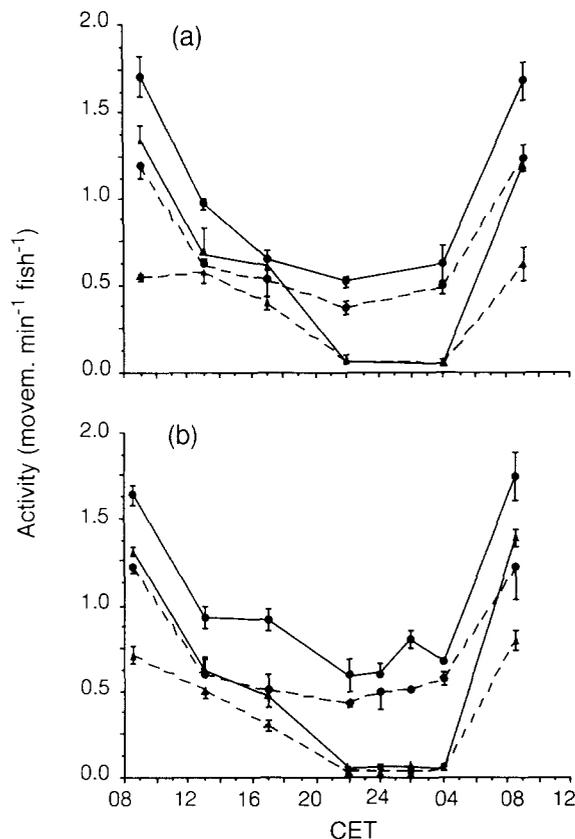
Fig. 6. Diel pattern in activity of juvenile turbot under two temperatures and two photoperiods. (a) 19-26 March, (b) 16-23 April. ▲=LDN, ●= LD24:0. Broken lines = 10°C, solid lines = 16°C. CET=Central European Time.

explain why size classes have different spatial distribution pattern.

Continuous light enhanced the growth rate above that of other light regimes in the present study, in accordance with earlier findings on other fish species. This growth enhancement was significant at 10°C from mid-December to late March, and from mid-December to late January at 16°C. A growth-promoting effect of extended day length and continuous light is well documented for salmonids in freshwater (Saunders et al., 1985; Stefansson et al., 1989; Berg et al., 1992) and postsmolts in seawater (Kråkenes et al., 1991). Similar results have been found in studies with some marine fish (Fonds, 1979; Boehlert, 1981; Folkvord & Otterå, 1993). In the present study, however, the overall effects of photoperiod were less pronounced and the duration of the growth enhancement at continuous light shorter than previous studies on anadromous species, suggesting that juvenile turbot have a photo-response which differs from that of anadromous species.

Turbot can be found from North Africa and the Mediterranean to the Northeast Atlantic (Nielsen, 1973), an area characterized by seasonal changes in day length. Juvenile turbot are observed in large numbers in the surf zone of beaches (Liewes, 1984), where they are frequently found within a depth of 2 m and thus are exposed to intense sunlight and long days in summer. In a study of the ecology of young turbot at Borth, Wales, Jones (1973) found that growth showed a distinct seasonal pattern. The growth was rapid in summer, and very slow in winter. He concluded that this growth pattern was mainly regulated by temperature, although he suggested that other factors such as day length might be involved. Some studies on other flatfish have, however, not revealed any significant effect of photoperiod on growth (sole, Fuchs, 1978; Atlantic halibut, Hippoglossus hippoglossus, Hallaråker et al., 1995). In contrast, Fonds (1979) reported seasonal variation in growth rate of sole and plaice reared under natural light regime and at constant temperature. Some effects of photoperiod on growth rate have been found in other marine species (Boehlert, 1981; Folkvord & Otterå, 1993), but these findings and those reported by Fonds (1979) are not as dramatic as those found in anadromous species (Stefansson et al., 1989, 1991; Berg et al., 1992).

Studies with anadromous species have shown the importance of photoperiod as a 'zeitgeber' for endogenous rhythms influencing growth rate and rate of development (Eriksson & Lundqvist, 1982; Stefansson et al., 1989). The marine environment as a whole is characterized by seasonal changes in external factors which are lower in magnitude than those found in shallow lakes and streams. The importance of photoperiod as a 'zeitgeber' for endogenous rhythms influencing growth rate could thus be expected to be somewhat less in the marine environment than in the freshwater environment. The results of the present study and results from other growth studies on marine species (Fuchs, 1978; Fonds, 1979; Boehlert, 1981; Folkvord & Otterå, 1993; Hallaråker et al., 1995) support the hypothesis of a reduced growth-promoting effect of photoperiod on marine species as compared with freshwater species.

In a study with wild caught juvenile halibut Haug et al. (1989) reported a seasonal change in condition index with lower K in winter. The results from the present study also indicate seasonal changes in growth and condition index in juvenile turbot, in accordance with these earlier findings on flatfish in nature. The condition index was significantly lower in winter than in late autumn and early spring. At both temperatures the LD24:0 groups had highest K in winter indicating that these groups added more somatic tissue than the other experimental groups. In nature seasonal changes in growth have been seen in halibut (Sigurdsson, 1956) and in turbot (Jones, 1973), with more rapid growth in summer and autumn than in winter.

Photoperiod affected the oxygen consumption of juvenile turbot. This was most clearly demonstrated at night when the LD24:0 groups invariably had a higher O_2 consumption than the LDN and LD16:8 groups at corresponding temperatures. Studies on the relationship between photoperiod and oxygen consumption in fish are scarce. Waller (1992) studied the oxygen consumption of juvenile turbot in relation to season. He found that the O_2 consumption during the evening and night was higher in summer than in winter and suggested that this was due to changes in both temperature and photoperiod. The results of the present study are thus in agreement with his findings. The exposure of fish to continuous light may have affected the oxygen consumption directly by altering the level of activity.

Several studies on fish activity (Verheijen & De Groot, 1967; Gibson, 1973; Müller, 1978; Fernö et al., 1986) show that low activity is to be expected at night. In turbot, inactive phases at night alternate with active phases during the day (Champalbert et al., 1989; Waller, 1992). In the present study the activity of the fish in the LDN groups was very low at night, whereas in the LD24:0 groups the nocturnal activity was always significantly higher than for the LDN groups. Thus, it seems evident from the present study that photoperiod directly affects the activity pattern of turbot by altering the nocturnal activity. This is in accordance with Eriksson (1978), who reported that in brown bullhead, Ictalurus nebulosus, there was a direct effect of photoperiod on the amount of activity. Kryuchkov et al. (1989) studied the daily periodicity of motor activity of the common carp, Cyprinus carpio, and concluded that photoperiod exerts a strong influence on motor activity. In some species photoperiod exerts a stronger influence on motor activity than does temperature (Müller, 1978; Kryuchkov et al., 1989). Evidence from the present study indicates that extended photoperiod does indeed exert a strong influence on activity in juvenile turbot.

5. SYNOPSIS

A growth-promoting effect of continuous light was seen in the LD24:0 groups but the duration of this growth enhancement was limited, especially at 16°C. Greater activity and higher oxygen consumption were seen in the LD24:0 groups, coinciding with low growth rate in the LD24:0-16°C groups compared to growth rate in the LDN and LD16:8 groups.

Boehlert (1978) reported that juvenile splitnose rockfish acclimated to short photoperiods had higher standard metabolic rates than those acclimated to long photoperiods at the same temperature. He found enhanced growth of the fish in the longer photoperiod and suggested that the enhanced growth could be related to a greater scope for growth. In contrast to Boehlert (1978), the oxygen consumption of the LD24:0 groups was higher than that of the LDN and LD16:8 groups, while the growth rate of the LD24:0-

16°C group was lower than growth rate in the LDN-16°C and LD16:8-16°C groups. A possible explanation could be that the lower growth rate in the LD24:0-16°C group from January onwards, than in the LDN-16°C and LD16:8-16°C groups, is related to a limited scope for growth as a consequence of higher metabolic rates.

The activity of fish is reflected in their oxygen consumption and energy demand (Beamish & Mookherjii, 1964). In this study the fish in the LD24:0 groups showed greater overall activity than the fish in the LDN groups. An increased energy demand as a consequence of increased activity has been confirmed in several studies (Nahhas et al., 1982; Butler, 1985). Consequently, because of their greater activity, the LD24:0 groups would have the highest energy demand. The fish were not fed at night, but a considerable activity was noted in the LD24:0 groups. This may have led to an inadequate fulfilment of the energy requirements of the fish in these groups and limited their scope for growth. However, in nature when juvenile turbot live in shallow water at high latitudes (Jones, 1973) they will presumably have access to food during the entire period of light. Therefore, an investigation is needed on the effect of continuous feeding, or several feedings over the 24-hour cycle, when juvenile turbot is reared under LD24:0 conditions.

6. REFERENCES

Anthony, T., 1910. The cultivation of the turbot. Proc. Fourth Int. Fish. Congr., Washington, 1908.—Fish. Bull. U.S. **28**: 859-870.

Beamish, F.W.H. & P.S. Mookherjii, 1964. Respiration of fishes with special emphasis on standard oxygen consumption. II. Influence of weight and temperature on respiration of goldfish, Carassius auratus L.—Can. J. Zool. **42**: 161-175.

Berg, L., V. Baarøy, D.S. Danielsen, T. Van der Meeren, K.E. Naas, K. Senstad & V. Øiestad, 1985. Production of juvenile flatfish species in different sized mesocosms. ICES C.M. 1985/F:65: 1-18.

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.

Boehlert, G.W., 1978. Changes in the oxygen consumption of prejuvenile rockfish, Sebastes diploproa, prior to migration from the surface to deep water.—Physiol. Zool. **51**: 56-67.

——, 1981. The effects of photoperiod and temperature on laboratory growth of juvenile Sebastes diploproa 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.

Brix, O., 1992. Oxygen uptake. In: K. Døving & E. Reimers. Fiskens fysiologi. John Grieg Forlag A/S, Bergen: 174-182 (in Norwegian).

Bromley, P.J., 1979. The weaning of turbot (*Scophthalmus maximus* L.) and sole (*Solea solea* L.) on dry diets. In: J.E. Halver & K. Tiews. Finfish nutrition and fishfeed technology. Heenemann Verlagsgeselleschaft, Berlin: 449-455.

Bromley, P.J. & P.A. Sykes, 1985. Weanings diets for turbot (*Scophthalmus maximus* L.), sole (*Solea solea*) (L.) and cod (*Gadus morhua* L.). In: C.B. Cowey, A.M. Mackie & J.G. Bell. Nutrition and feeding in fish. Academic Press, Aberdeen: 191-211.

Brown, M.B. & A.B. Forsythe, 1974. Robust tests for the equality of variances.—J. Am. Stat. Assoc. **69**: 364-367.

Butler, P.J., 1985. Exercise in non-mammalian vertebrates: a review.—J. R. Soc. Med. **78**: 739-747.

Champalbert, G., C. Castelbon, L. Le Direach-Boursier & A. Bourdillon, 1989. Locomotory activity rhythms in juvenile *Solea vulgaris* and *Scophthalmus maximus* L.—Rapp. P.-v. Réun. Cons. perm. int. Explor. Mer **191**: 486.

Eriksson, L.-O., 1978. Nocturnalism *versus* diurnalism - dualism within fish individuals. In: J.E. Thorpe. Rhythmic activity of fishes. Academic Press, London: 69-89.

Eriksson, L.-O. & H. Lundqvist, 1982. Circannual rhythms and photoperiod regulation of growth and smolting in Baltic salmon (*Salmo salar* L.).—Aquaculture **28**: 113-121.

Fernö, A., P. Solemdal & S. Tilseth, 1986. Field studies on the behaviour of whiting (*Gadus merlangus* L.) towards baited hooks.—FiskDir. Skr. Ser. Havunders. **18**: 83-95.

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. Proc. 13th Eur. Mar. Biol. Symp. Pergamon Press, New York: 151-156.

Fuchs, J., 1978. Influence de la photoperiode sur la croissance et la survie de la larve et du juvenile de sole (*Solea solea*) en elevage.—Aquaculture **15**: 63-74.

Gibson, R.N., 1973. Tidal and circadian activity rhythms in juvenile plaice, *Pleuronectes platessa*.—Mar. Biol. **22**: 379-386.

Gross, W.L., E.W. Roelofs & P.O. Fromm, 1965. Influence of photoperiod on growth of green sunfish, *Lepomis cyanellus*.—J. Fish. Res. Bd Can. **22**: 1379-1386.

Hallaråker, H., A. Folkvord & S.O. Stefansson, 1995. Growth of juvenile halibut (*Hippoglossus hippoglossus*) related to temperature, day length and feeding regime.—Neth. J. Sea Res. **34**: 139-147.

Hansen, E.H., 1990. Bruk av kunstig lys og lysmanipulering for styrt produksjon av laksefisk. Dr. ing. thesis. Norwegian Institute of Technology, University of Trondheim: 1-137 (in Norwegian).

Haug, T., I. Huse, E. Kjørsvik & H. Rabben, 1989. Observations on the growth of juvenile Atlantic halibut (*Hippoglossus hippoglossus* L.) in captivity.—Aquaculture **80**: 79-86.

Heap, S.P. & J.P. Thorpe, 1987. A preliminary study of comparative growth rates in 0-group malpigmented and normally pigmented turbot, *Scophthalmus maximus* (L., and turbot-brill hybrids, *S. maximus* X *S. rhombus* (L.), at two temperatures.—Aquaculture **60**: 251-264.

Holt, E.W.L., 1892. *Rhombus maximus*, Linn. (The turbot).—J. mar. biol. Ass. U.K. **2**: 399-404.

Houde, E.D. & R.C. Schekter, 1981. Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations.—Rapp. P.-v. Réun Cons. perm. int. Explor. Mer **178**: 441-453.

Howell, B.R., 1979. Experiments on the rearing of larval turbot, *Scophthalmus maximus* L.—Aquaculture **18**: 215-225.

Iglesias, J., M. Olmedo, J.J. Otero, J.B. Peleteiro & M.R. Solórzano, 1987. Growth, under laboratory conditions, of turbot, *Scophthalmus maximus*, from the Ría de Viga (north-west Spain).—Mar. Biol. **96**: 11-17.

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

Jones, A., 1972. Studies on egg development and larval rearing of turbot, *Scophthalmus maximus* L., in the laboratory.—J. mar. biol. Ass. U.K. **52**: 965-986.

——, 1973. The ecology of young turbot, *Scophthalmus maximus* (L.) at Borth, Cardiganshire, Wales.—J. Fish Biol. **5**: 367-383.

Jones, A., J.A.G. Brown, M.T. Douglas, S.J. Thompson & R.J. Whitfield, 1981. Progress towards developing methods for the intensive farming of turbot (*Scophthalmus maximus* L.) in cooling water from a Nuclear Power Station. In: K. Tiews. Aquaculture in heated effluents and recirculation systems. Tech. Pap. FAO, Stavanger, Vol. 16-17: 481-496.

Kilambi, R.V., J. Noble & C.E. Hoffman, 1970. Influence of temperature and photoperiod on growth, food consumption, and food conversion efficiency of channel catfish. Proc. Ann. Conf. Southeast. Assoc. Game. Fish Comm. 24th: 519-531.

Kråkenes, R., T. Hansen, S.O. Stefansson & G.L. Taranger, 1991. Continuous light increases growth rate of Atlantic salmon (*Salmo salar* L.) postsmolts in sea cages.—Aquaculture **95**: 281-287.

Kryuchkov, V.I., R. Yu. Kasimov, B.F. Tsonif & T.A. Mamedova, 1989. Daily rhythm of motor activity of young of the mirror carp, *Cyprinus carpio*, under various regimes of illumination and temperature.—J. Ichthyol. **29**: 150-155.

Liewes, E.W., 1984. Culture, feeding and diseases of commercial flatfish species. Balkema, Rotterdam: 1-104.

Malard, A.E., 1899. Sur le développement et la pisciculture du turbot. C.R. Acad. Sci. Paris **129**: 181-183.

Müller, K., 1978. Locomotor activity of fish and environmental oscillations. In: J.E. Thorpe. Rhythmic activity of fishes. Academic Press, London: 1-19.

Nahhas, R., N.V. Jones & G. Goldspink, 1982. Some aspects of sustained training of rainbow trout, *Salmo gairdneri* Richardson.—J. Fish Biol. **20**: 351-358.

Nielsen, J.G., 1973. Scophthalminidae. In: J.-C. Hureau & T. Monod. Check-list of the fishes of the North-eastern Atlantic and of the Mediterranean. Vol. 1. UNESCO, Paris: 616-619.

Person-Le Ruyet, J., J. Barret, D. L'Elchat & G. Nedelec, 1981. Research on rearing turbot (*Scophthalmus max-*

imus): results and perspectives.—J. World Maricul. Soc. **12**: 143-152.

Purdom, C.E., A. Jones & R.F. Lincoln, 1972. Cultivation trials with turbot (*Scophthalmus maximus*).—Aquaculture **1**: 213-230.

Roberts, R.J., 1993. Motile *Aeromonad septicaemia*. In: V. Inglis, R.J. Roberts & N.P. Bromage. Bacterial diseases of fish. Blackwell Scientific Publications, London: 143-155.

Saunders, R.L. & P.R. Harmon, 1988. Extended daylength increases postsmolt growth of Atlantic salmon.—World Aquaculture **19**: 72-73.

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.

Saunders, R.L., J.L. Specker & M.P. Komourdjian, 1989. Effects of photoperiod on growth and smolting in juvenile Atlantic salmon (*Salmo salar*).—Aquaculture **82**: 103-117.

Scheffé, H., 1959. The analysis of variance. John Wiley & Sons, New York: 1-477.

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., N.S. **1**(16): 1-24.

Smith, P.L., 1976. The development of a nursery technique for rearing turbot, *Scophthalmus maximus*, from meta-morphosis to ongrowing size. Progress since 1970 by the British white fish authority. FAO Technical Conference On Aquaculture, Kyoto, Japan, 26 May-2 June 1976: 1-13.

Sokal, R.R. & F.J. Rohlf, 1981. Biometry. 2nd edition. Freeman, San Francisco: 1-859.

Stefansson, S.O., G. Nævdal & T. Hansen, 1989. The influence of three unchanging photoperiods on growth and parr-smolt transformation in Atlantic salmon, *Salmo salar* L.—J. Fish Biol. **35**: 237-247.

Stefansson, S.O., B.Th. Bjørnsson, 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.

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

Verheijen, F.J. & S.J. De Groot, 1967. Diurnal activity pattern of plaice and flounder (*Pleuronectidae*) in aquaria.—Neth. J. Sea Res. **3**: 383-390.

Waller, U., 1992. Factors influencing routine oxygen consumption in turbot, *Scophthalmus maximus*.—J. appl. Ichthyol. **8**: 62-71.

Zar, J.H., 1984. Biostatistical analysis. 2nd edition. Prentice-Hall, Englewood Cliffs: 1-718.