Sexual dimorphism in growth and maturation of turbot, *Scophthalmus maximus* (Rafinesque, 1810)

A K Imsland, A Folkvord, G L Grung & S O Stefansson
Department of Fisheries and Marine Biology, University of Bergen, Bergen, Norway

G L Taranger
Institute of Marine Research, Department of Aquaculture, Bergen, Norway

Correspondence: Dr Albert K Imsland, Department of Fisheries and Marine Biology, University of Bergen, High Technology Centre, N–5020 Bergen, Norway

Abstract

Sexual dimorphism in growth and maturation of individually tagged turbot ($n = 421$), *Scophthalmus maximus* Rafinesque, was studied in a long-lasting (20 months) growth experiment with four temperature regimes. The influence of onset of puberty and subsequent maturation on growth was evaluated. There were no initial size differences, but the final weight of females was larger than that of males at all temperature regimes, except at the lowest temperature. Surplus energy (sum of increase in somatic weight and gonad weight) in females was on average greater than in males from 8 months prior to first spawning. Significant growth (as specific growth rate, SGR) differences between maturing and immature fish were detected from the age of 9 months post hatch. Maturing females had the highest growth rate and reached the largest size (1.8 kg in 20 months), whereas male body weights reached a plateau and levelled off around 1.0 kg. To optimize production characteristics in turbot aquaculture and achieve more homogeneous growth, methods should be developed to produce all-female broods.

Introduction

Turbot, *Scophthalmus maximus* Rafinesque, is one of the most promising candidates for marine aquaculture in Europe. However, large individual variations in growth performance have been observed in turbot (Rosenberg & Haugen 1982; Nijhof 1994; Imsland, Folkvord & Stefansson 1995) and there is a need to optimize production characteristics (Lavens & Remmerswaal 1994). To achieve more homogenous growth, one needs to control factors that significantly contribute to growth variation in turbot. One of these factors is sexual dimorphism in growth potential (Purdom, Jones & Lincoln 1972; Devauchelle, Alexandre, Le Corre & Letty 1988).

Sexual dimorphism in size has been observed and studied in many species. Males normally become larger than females in many members of the order Salmoniformes, including rainbow trout, *Oncorhynchus mykiss* (Walbaum) (Nævdal, Holm, Lerøy & Møller 1979; Elvinson & Johansson 1993), Atlantic salmon, *Salmo salar* L. (Nævdal, Lerøy & Møller 1983) and chinook salmon, *Oncorhynchus tshawytscha* (Walbaum) (Peterson, Winkelman, Devlin & Harrower 1992). Where breeding is frequent and not connected to season, as in many tropical species, males are also reported to be larger than females. This includes many cichlids, e.g. the Nile tilapia, *Oreochromis niloticus* (L.) (Lowe-McConnell 1987), and some threadfin breams, e.g. *Nemipterus japonicus* Bloch, 1791 (Samuel 1986).

In contrast, females are larger than males in many species of the order Gadiformes e.g. roundnose grenadier, *Coryphaenoides rupestris* Gunnerus, 1765 (Bergstad 1990) and Pacific whiting, *Merluccius productus* (Ayres) (Dorn 1992). Larger females are also reported in the order Anguilliformes e.g. European eel, *Anguilla anguilla* L. (Panfili, Ximénès & Crivelli 1993), as well as in many families of Pleuronectiformes [Soleidae (De Veen 1976);

Psettodidae (Druzhinin & Petrova 1980); Pleuronectidae (Berner & Sager 1985); Bothidae (Déniel 1990)]. Earlier studies in teleosts have shown that there is a significant correlation between the life history parameters, age at first reproduction, natural mortality, and growth rate. The mathematical models of Charlesworth & León (1976), Roff (1983, 1991) and Stearns (1992) emphasize that these correlations are the result of evolutionary adjustments due to the trade-off between reproduction, growth and survival. According to these models, both growth rate and survival will decrease with increasing reproductive effort. It is well established that fecundity increases with size (Bagenal 1966; Wootton 1979). Energy channelled into the gonads detracts from somatic growth and hence future fecundity (Ware 1980; Roff 1983). Hence, there exists a direct trade-off between growth and reproduction, but this trade-off can vary between the sexes (Craig 1977; Rijnsdorp & Ibelings 1989).

Some reports on flatfish have concluded that the sum of increases in somatic weight and gonad weight, i.e. surplus energy (energy in excess of maintenance requirements, Ware 1978), of both sexes is equal up to a particular size, but beyond that size females have greater surplus energy than males [plaice, *Pleuronectes platessa* L., Rijnsdorp & Ibelings (1989); dab, *Limanda limanda* L., Lozán (1992)]. Female growth is thus far in excess of the males after the attainment of sexual maturity [e.g. turbot, Devauchelle *et al.* (1988); Atlantic halibut, *Hippoglossus hippoglossus* (L.), Jákupsstovu & Haug (1988), Björnsson (1995)]. But it still remains unknown whether the growth patterns of the sexes are different in the juvenile stage, and whether there is already a greater surplus energy in females than in males at immature stages.

To examine the sexual dimorphism in growth and maturation in turbot, a growth experiment lasting 20 months was performed. Further, to analyse the phenotypic plasticity of maturation, the fish were reared under four different temperature regimes and individual growth trajectories of the fish were followed. Maturity status and its influence on growth was assessed as gonads were sampled from the fish throughout the juvenile phase until first spawning.

Material and methods

Biological material and experimental design

Eggs from one female turbot were fertilized with the pooled sperm from two males on 7 July 1991. After hatching, the larvae were transferred to 8.0-m^3 plastic bags floating in a seawater basin. From 16 July the larvae were fed natural zooplankton filtered from the basin. After metamorphosis the juveniles were transferred to indoor 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 17 January 1992 until 24 August 1993. Initially, the experimental tanks were 1 m^2 and square; later (see below) the fish were 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 measured weekly in the effluent water of all tanks and was above 75% at all times. The fish were fed from automatic feeders every 4 min during the photophase. All groups were fed commercial dry feed (Marin pellets 2–9 mm; Felleskjøpet AS, Bergen) in excess, and the amounts fed were adjusted after each weighing based on previous growth rates (% biomass + 1%).

On 7 November 1991 the fish were transferred from the holding temperature of 13°C directly to the four experimental temperatures of 10°C, 13°C, 16°C and 19°C. On 17 January 1992 (19°C) and 30 January 1992 (10°C, 13°C, 16°C) a total of 421 randomly chosen fish from the temperature groups (Table 1) were individually tagged with Fisheagle® PIT tags (Prentice, Park, Flagg & McCutcheon 1986). All growth analyses presented in the present paper are based on those individually tagged fish (179 females and 242 males). Part of the fish at 10°C and 16°C were reared under constant photoperiods (Imsland *et al.* 1995), the numbers of fish in each group in the present study were not equal (Table 1). On 26 May 1992 rearing at 13°C and 19°C was discontinued, and the fish from these temperatures were combined with the remaining fish held at 10°C and 16°C respectively (Table 1) throughout the experimental period. Four experimental regimes were thus established, 10/10°C, 13/10°C, 16/16°C, and 19/16°C. Temperatures were measured twice daily, and remained within ± 0.2°C of the prescribed value throughout the experimental period. Sexual maturation was evaluated by palpation of the abdomen of the fish at all weighing times in 1993 and checking for running milt or roe. In 1993 all fish within each temperature regime were grouped into four categories based on maturation status, i.e.

Table 1 Overview of the experimental set-up, number of fish in each experimental group and mortality within each group. Number indicates number of individually tagged fish in each category within each temperature regime. The gonad samples were mainly taken from untagged fish reared under 13/10°C and 19/16°C temperature regimes

Temp. regime (°C)	Sex and maturing status	Temperature (°C) in each rearing period		Number of fish		Mortality[2] (%)
		Jan. 1992 – May 1992	May 1992 – Aug. 1993	Start	Final[1]	
10/10	Female, non-maturing	10	10	12	11	0
	Female, maturing	10	10	5	5	0
	Male, non-maturing	10	10	12	12	0
	Male, maturing	10	10	4	4	0
13/10	Female, non-maturing	13	10	63	60	1
	Female, maturing	13	10	10	9	0
	Male, non-maturing	13	10	100	92	2
	Male, maturing	13	10	17	11	0
16/16	Female, non-maturing	16	16	7	6	0
	Female, maturing	16	16	10	9	0
	Male, non-maturing	16	16	10	8	10
	Male, maturing	16	16	7	6	0
19/16	Female, non-maturing	19	16	38	24	1
	Female, maturing	19	16	34	31	1
	Male, non-maturing	19	16	56	45	0
	Male, maturing	19	16	36	31	0

[1]The last date on which all groups can be compared is 2 April 1993, and this date is thus defined as the final date in this context.

[2]Mortality does not include fish that were sacrificed during gonad sampling.

maturing females (F1), maturing males (M1), non-maturing females (F0) and non-maturing males (M0). Further, biopsy samples were taken from non-maturing fish to determine the sex of these fish.

Data analyses and statistical methods

Weighing was conducted every 2 weeks until 26 May 1992, monthly until August 1992 and every 2 months thereafter. All fish were weighed individually to the nearest 0.01 g. Specific growth rate (*SGR*, %) was calculated according to the formula of Houde & Schekter (1981):

$$SGR = (e^g - 1) * 100 \qquad (1)$$

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. From August 1992, gonad samples were taken from randomly chosen fish of the untagged subpopulation held at the 13/10°C and 19/16°C temperature regimes. Initially, 10 fish from each group were sampled, but this was later increased to 20 fish

from each group. Gonadosomatic index (*GSI*) was calculated as:

$$GSI = (\text{gonad weight/total wet weight}) * 100. \qquad (2)$$

Some individually tagged fish were also killed during gonad sampling, and were considered mature or maturing (for growth analysis) if their *GSI* was $\geqslant 2 \times$ mean *GSI* at the sampling date. Gonad sampling was conducted monthly, apart from the period August 1992–December 1992 when sampling was conducted every second month. Changes in gonad weight were used to classify the fish as being in previtellogenesis, early or late vitellogenesis, in agreement with data previously reported on turbot (Jones 1974; Devauchelle *et al.* 1988; Soengas, Barciela & Aldegunde 1995). Surplus energy (i.e. energy in excess of maintenance requirements, Ware 1978, 1980) was calculated as the sum of the increases in somatic weight and gonad weight:

$$\Delta S = (W_{t+1} - W_t) + G_{t+1}$$
$$\text{(rearranged from Roff 1983)} \qquad (3)$$

where W_t and W_{t+1} are somatic weights at time t and $t+1$ respectively, ΔS is the surplus energy for the time period from t to $t+1$, and G_{t+1} is the weight of the gonads at time $t+1$. Here, G_t is considered to be negligible at time t.

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 (Zar 1984). The mean weights of the different maturation groups at different measurement dates were tested in a one-way model I analysis of variance (ANOVA). Significant ANOVAs were followed by a Student–Newman–Keuls multiple comparison test to determine differences among experimental groups. Individual growth trajectories for all fish at each temperature regime 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:

$$\mathbf{Y}(n \times p) = \mathbf{X}(n \times q)\mathbf{B}(q \times p) = \mathbf{E}(n \times p) \quad (4)$$

where: $\mathbf{Y}(n \times \mathrm{p})$ are the growth at age vectors $\mathbf{y} = (y_1, y_2, ..., y_p)$ for each p (age) measurements on n individual fish; $\mathbf{X}(n \times q)$ is the design matrix or the set of extraneous variables measured for each individual, i.e. $q = \mathrm{age}_p + \mathrm{group}_i$; ($i$ = non-maturing females, maturing females, non-maturing males, maturing males); $\mathbf{B}(q \times p)$ is the matrix of parameters estimated by the model; and $\mathbf{E}(n \times p)$ is the matrix of deviations for each individual from the expected value of $\mathbf{Y} = \mathbf{XB}$.

A two-way fixed covariance analysis (ANCOVA, Sokal & Rohlf 1995) was used to analyse which of the factors, sex, temperature regime, final size (April 1993), and average growth rate in every 3-month period from January 1992 to April 1993, influenced maturation of individual fish, and to see whether growth in the juvenile stage was related to the process of maturation. The model equation of the ANCOVA had the form:

$$y_{ij} = \mu + \alpha_i + (\alpha\gamma_{ij}) + \beta_1 x_{1ij} + \beta_2 x_{2ij} + \beta_3 x_{3ij} + \beta_4 x_{4ij} + \beta_5 x_{5ij} + \beta_6 x_{6ij} + \varepsilon_{ij} \quad (5)$$

where: μ is the overall mean; α_i and γ_j are the treatment effects of sex and temperature regime, respectively; $\alpha\gamma_{ij}$ is the interaction of sex and temperature regime; β_1–β_6 are the coefficients of the covariates size, average growth ($\overline{G}$) in months 7–9, $\overline{G}$ in months 10–12, $\overline{G}$ in months 13–15, $\overline{G}$ in months 16–18 and $\overline{G}$ in months 19–22, respectively.

Month 0 is defined as July 1991 (hatching) and month 7 is January 1992; and ε_{ij} is the error term.

Correlation between growth rate and gonadosomatic index was assessed using the correlation coefficient (Zar 1984). Weight-frequency distributions were tested for dispersions from normality using the Kolmogorov–Smirnov test and applying the critical values suggested by Stephens (1974). Data on maturity proportion of the sexes were tested in a 2×2 contingency-table chi-square test (Zar 1984). A significance level (α) of 0.05 was used if not stated otherwise. In non-significant cases, power $(1-\beta)$ analyses for those tests were performed according to the methods described in Zar (1984) using $\alpha = 0.05$.

Results

Mortality

One male (group M0) died at the 16/16°C temperature, and due to the low number of immature males this amounted to 10% mortality. Apart from this, mortality was low in all experimental groups (0–2%, Table 1). No sex- or size-specific mortality was recorded (χ^2 test, $P > 0.7$).

Growth in relation to sex and maturation

The sexes differed clearly in their growth patterns (Figs 1 and 2). Females were larger than males in all temperature regimes except for the 10/10°C regime (Fig. 1). At 10/10°C, maturing males were largest of all categories but this result is based on very few fish ($n = 4$), which may partly explain this discrepancy. No significant differences were found at 10/10°C. Females reared at 19/16°C were larger than other groups at that temperature regime from early March 1992 and onwards (Fig. 1d, one-way ANOVAs, $P < 0.01$). At 16/16°C and 13/10°C, females were larger than males from July 1992; in both these groups, females displayed highest final weight and were significantly larger (Fig. 1c, one-way ANOVAs, $P < 0.05$) from February 1993 (16/16°C) onwards, and between December 1992 (Fig. 1b, one-way ANOVA, $F_{3, 194} = 3.42$, $P < 0.05$) and April 1993 (one-way ANOVA, $F_{3, 174} = 3.12$, $P < 0.05$).

Maturing and non-maturing fish also differed markedly in their growth pattern (Fig. 1). Initially no size differences within each experimental
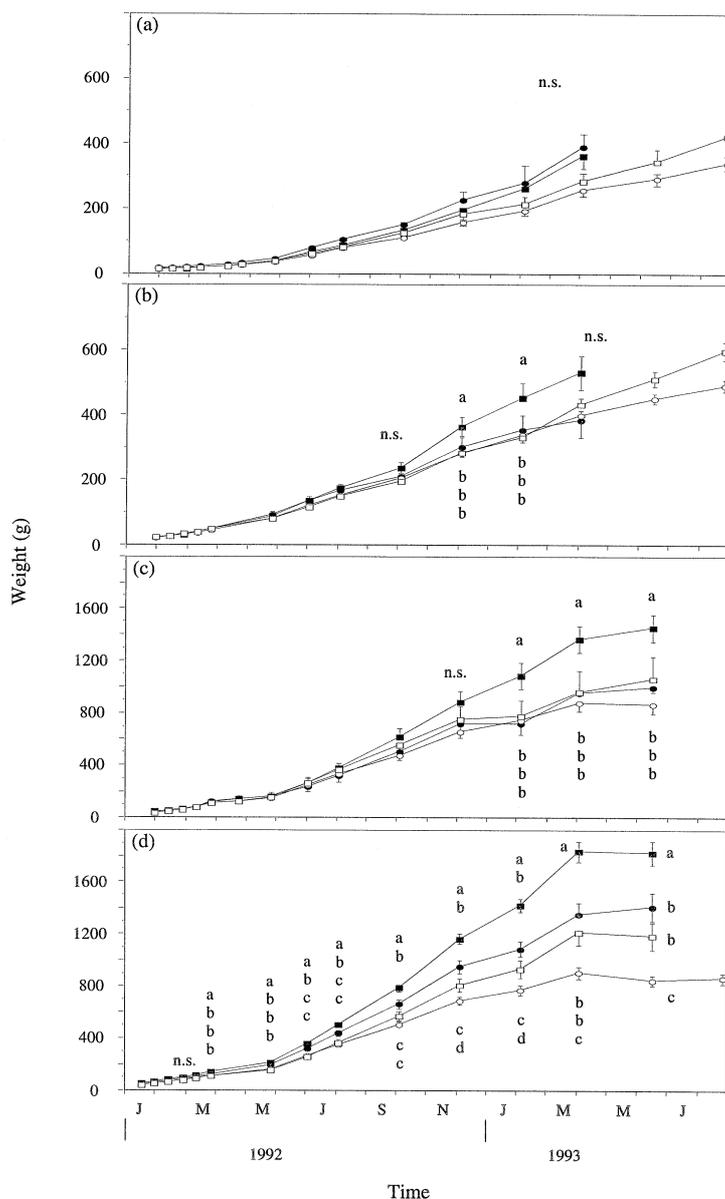
Figure 1 Mean weights of individually tagged turbot in four temperature regimes: (a) 10/10°C; (b) 13/10°C; (c) 16/16°C; (d) 19/16°C. ■, Maturing females; ●, maturing males; □, non-maturing females; ○, non-maturing males. Vertical lines indicating standard errors (SE) of the means may be obscured by the symbols. Different letters denote significant differences (one-way ANOVA) within each weighing period; n.s., not significant. Note differing vertical scales.

temperature were found (Fig. 1, one-way ANOVA, $P > 0.27$, 1-β > 0.65). However, from August 1992, maturing fish were larger than non-maturing fish in all experimental temperatures (Fig. 1). At 13/10°C, 16/16°C and 19/16°C, maturing females were the largest fish overall (Fig. 1b, c and d) from July 1992 and throughout the experimental period. Non-maturing males had the lowest final weight (one-way ANOVA) in all groups except 13/10°C where M0 were slightly larger than maturing males (Fig. 1b). At all temperatures, non-maturing females

were larger than non-maturing males from October and onwards.

The GCM analysis revealed growth-at-age differences at all temperature regimes (Fig. 2). Individual growth-at-age trajectories at 13/10°C were different (Fig. 2c, MANOVA(GROUP), Wilk's lambda $(\Lambda)_{24, 374} = 0.723$, $P < 0.01$) between the four groups (F1, F0, M0 and M1) from early March 1992 to April 1993 (last date used in GCM analysis). At 19/16°C the groups had different growth-at-age trajectories from late March 1992 and onwards
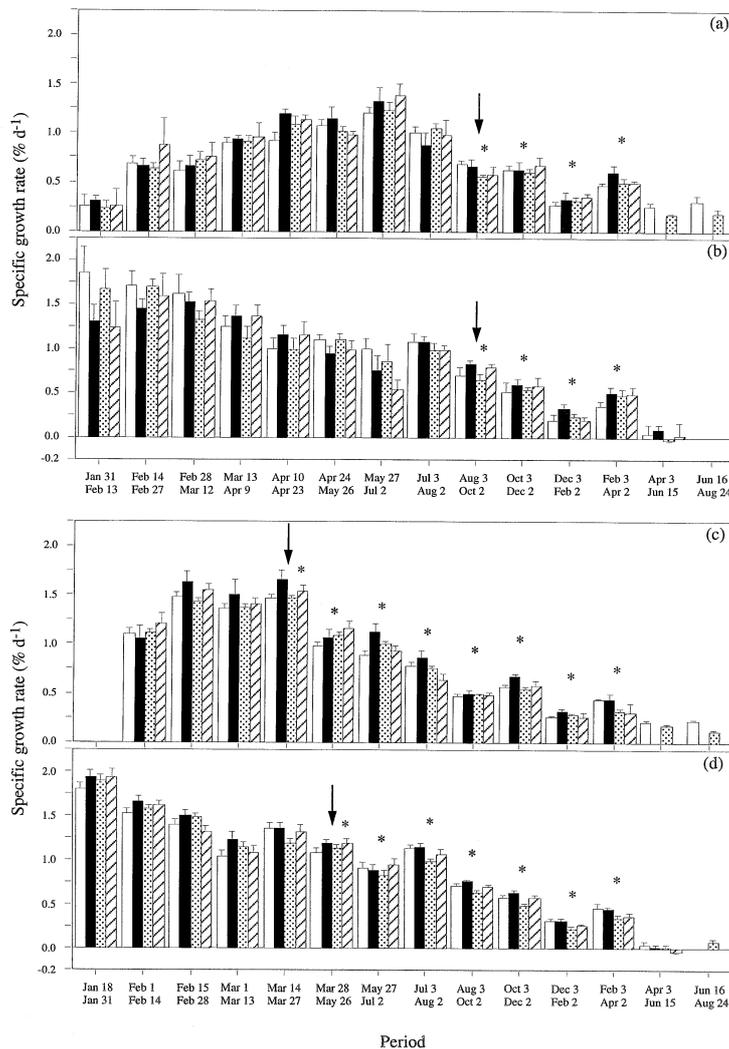
Figure 2 Mean (SE) specific growth rate of individually tagged turbot reared under four temperature regimes: (a) 10/10°C; (b) 16/16°C; (c) 13/10°C; (d) 19/16°C. □, Non-maturing females; ■, maturing females; ▦, non-maturing males; ▨, maturing males. Arrows mark the first time period where groups differ in growth rate (GCM MANOVA). Asterisks indicate significant difference in growth. Note differing horizontal axes.

(Fig. 2d, MANOVA(GROUP), Wilk's $\Lambda_{21,\ 299} = 0.731$, $P = 0.039$). The growth vectors of the fish reared at 10/10°C and 16/16°C differed significantly from August 1992 to April 1993 (10/10°C: MANOVA(GROUP), Wilk's $\Lambda_{12,\ 65} = 0.552$, $P < 0.05$; 16/16°C MANOVA(GROUP), Wilk's $\Lambda_{12,\ 57} = 0.495$, $P < 0.05$). In all significant MANOVAs (Fig. 2), maturing females had the highest average growth rate (0.62, 0.80, 0.55, 0.77% day^{-1} for 10/10°C, 13/10°C, 16/16°C and 19/16°C, respectively) whereas non-maturing males always displayed the lowest growth rate (0.49, 0.72, 0.44, 0.64% day^{-1}). Maturing males had also the second-highest growth rates at all temperatures except 19/16°C where non-maturing females had a higher growth rate than maturing males (Fig. 2). Growth rates in all groups at 16/16°C and 19/16°C were highest at the start of the experiment, decreasing throughout the experimental period (Fig. 2b and d). In contrast, growth rates at 10/10°C and 13/10°C were highest from May till July 1992 (10/10°C, Fig. 2a), and March 1992 (13/10°C, Fig. 2c), decreasing thereafter.

Size distribution

There were no differences in initial weight-frequency distribution of the categories at both 13/10°C and 19/16°C (Kolmogorov-Smirnov test, $P > 0.25$, Fig. 3a and e). However, by October 1992, most fish > 600 g at 19/16°C were
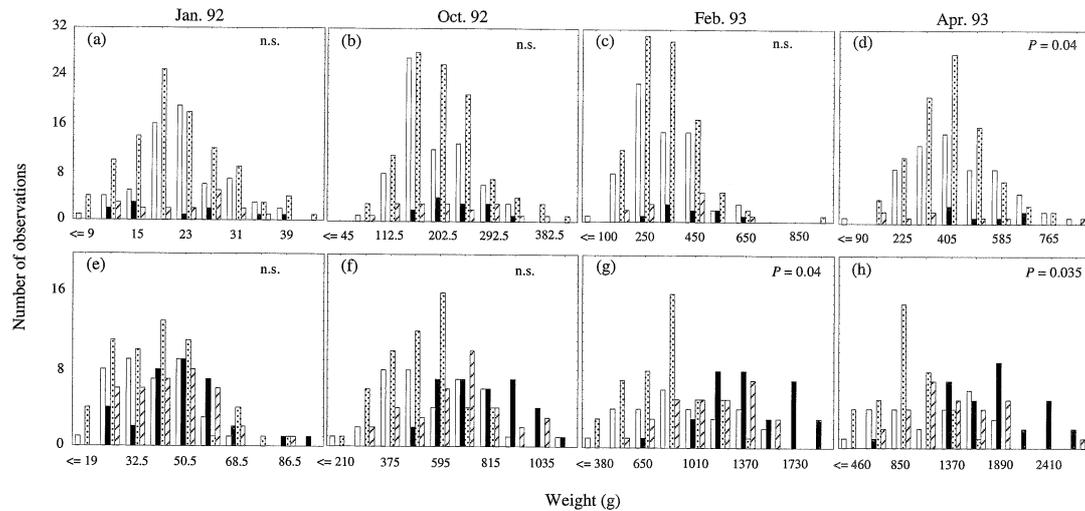
Figure 3 Weight-frequency distributions of individually tagged turbot at four different dates in 1992 and 1993: (a)–(d), temperature regime 13/10°C; (e)–(h), temperature regime 19/16°C. □, non-maturing females; ■, maturing females; ▦, non-maturing males; ▨ maturing males. *P* values for significant Kolmogorov–Smirnov test are given; n.s., not significant.

maturing (Fig. 3f), and in February and April 1993, dispersions from normal distribution indicating bimodality were found (Kolmogorov-Smirnov test, $P < 0.05$, Fig. 3g and h). Maturing fish at 13/10°C were mostly found in the upper part of the size range from October onwards (Fig. 3b, c and d), but as there were fewer maturing fish than at 19/16°C, size distribution differences were less pronounced. The final weight-frequency distribution was non-normal (Kolmogorov–Smirnov test, $P < 0.05$, Fig. 3d).

**Factors influencing maturation of females and males**

Overall, 29.2% of the fish in this study matured in 1993 (Table 1). The proportion of maturing fish (Table 1) was higher at 19/16°C (43%) and 16/16°C (50%) compared with 13/10°C (14%) and 10/10°C (27%). Maturity proportions did not differ between sexes within each temperature regime (2 × 2 contingency test, $\chi^2 < 1.3$, $P > 0.25$). Based on the analysis of covariance (ANCOVA, Table 2), maturation appeared to be mainly related to final body weight ($F_{1, 322} = 65.04$, $P < 0.0001$), temperature regime ($F_{3, 322} = 2.64$, $P = 0.048$), and mean growth rate between January and April 1993 ($F_{1, 322} = 3.90$, $P = 0.049$). There were no differences in maturation

between sexes ($F_{1, 322} = 0.004$, $P > 0.9$), nor were there any interaction effects between sex and temperature regime ($F_{3, 322} = 0.7$, $P > 0.5$). The model further suggests that differences in growth rate the year before maturation are related to maturation the year after, as the growth rate in January–March 1992 and July–September 1992 both tended towards significance ($P = 0.07$ and $P = 0.08$, respectively). The regression lines of both main factors were parallel for all covariates (Table 2, $P > 0.45$).

Specific growth rate of weight was negatively correlated with average gonadosomatic index in female turbot (Fig. 4, Pearson's $r = -0.58$, $P < 0.05$), and male turbot (Fig. 4, Pearson's $r = -0.62$, $P < 0.01$). Both gonadosomatic index (*GSI*) and surplus energy (ΔS) of the females (Table 3) rose steadily from August 1992, reaching a maximum in June 1993 and February 1993 respectively. Further, females nearly always displayed higher ΔS and *GSI* than males (Table 3). The *GSI* was higher at 19/16°C than at 13/10°C (Table 3). In males the average *GSI* never exceeded 0.9% of total weight and showed little variation with time (Table 3). Surplus energy decreased in both males and females between December 1992 and February 1993 (Table 3). In the late stages of maturation, both sexes at 19/16°C lost weight, and hence had negative ΔS (Table 3, Fig. 4).

Table 2 Analysis of covariance (ANCOVA) of maturity (y) in individually tagged female and male turbot as a function of body size in April 1993 (W in g) and average growth rate ($\Delta \overline{G}_i$ in % day^{-1}) in previous 3-month (i) period, and the main factors sex (S) and temperature regime (T); d.f., degrees of freedom

Source of variation	Sum of squares	d.f.	Mean square	*F*-ratio	*P*
Main effects					
Sex (S)	0.0006	1	0.0006	0.004	0.945
Temperature regime (T)	1.0693	3	0.3564	2.639	0.048
Interaction, main effects					
$S \times T$	0.2914	3	0.0971	0.700	0.552
Covariates					
Size (W)	9.0238	1	9.0238	65.047	<0.001
Growth rate 7–9 ($\overline{G}_{7-9}$)	0.4517	1	0.4517	3.256	0.070
Growth rate 10–12 ($\overline{G}_{10-12}$)	0.0972	1	0.0972	0.701	0.402
Growth rate 13–15 ($\overline{G}_{13-15}$)	0.4118	1	0.4118	3.050	0.082
Growth rate 16–18 ($\overline{G}_{16-18}$)	0.1444	1	0.1444	1.041	0.308
Growth rate 19–22 ($\overline{G}_{19-22}$)	0.5411	1	0.5411	3.900	0.049
All covariates	11.5115	6	1.9185	13.830	<0.001
Parallelism of covariates					
$S \times$ covariates	0.6073	6	0.1012	0.7260	0.629
$T \times$ covariates	2.4606	18	0.1367	0.9845	0.477
Error	44.6698	322	0.1387		
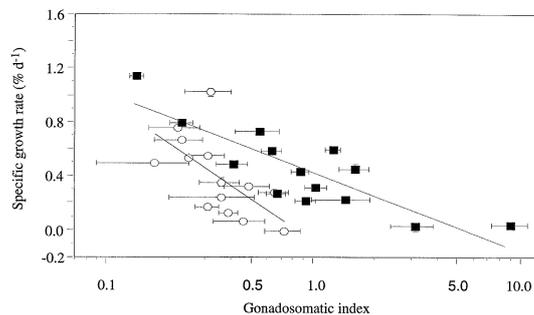
Figure 4 Specific growth rate (*SGR*) plotted against gonadosomatic index (*GSI*) for female (■) and male (○) turbot. The vertical and horizontal lines indicating SE may be obscured by the symbols.

Discussion

Females grew better than males in the present study in accordance with earlier studies on turbot (Jones 1974; Robert & Vianet 1988; Déniel 1990), and other flatfish species (Druzhinin & Petrova 1980; Jákupsstovu & Haug 1988; Miller, Burke & Fitzhugh 1991). Final weight of males was 94%, 89%, 76% and 72% of the mean final weight of females at 10/10, 13/10, 16/16 and 19/16°C regime, respectively (Fig. 1). One possible explanation of the observed sexual growth divergence might be differences in food intake. To explain observed sexual growth differences of dab, Lozán (1992) studied the food intake and digestive tract size of females and males. He found that on average, females consumed 73% more food than similar-sized males, and that females had a significantly larger digestive tract than males. He concluded that because of these differences females would grow better than males. It is thus possible that part of the observed growth differences seen in the present study originate from different food intake.

Another possible explanation of growth differences observed here are sex-related maturity differences influencing growth. Histological data on flatfishes indicate that the process of maturation could span a period of 2–3 years (Jones 1974; Burton & Idler 1984; Déniel 1984; Rijnsdorp 1989). In the present study, significant growth and size differences between the maturing and non-maturing fish (Figs 1 and 2) were found from 8 months after hatching. It was also clearly demonstrated that maturity was size dependent (Table 2), so that faster-growing turbot within each temperature regime matured earlier than slow-growing ones. It is further generally assumed that fish mature when they have passed a size or age threshold (Alm 1959; Roff 1982; Stearns 1992). Under intensive culture, rearing with high-energy feed available at all times and better

Table 3 Comparison of weight, gonadosomatic index (*GSI*) and surplus energy (Δ*S*) of female and male turbot from August 1992 to August 1993. Gonads were sampled from fish reared at two temperature regimes: 13/10°C and 19/16°C. *n* = 5–10 fish from each experimental group at each measurement date. Female maturation stage: PV, previtellogenesis; EV, early vitellogenesis; LV, late vitellogenesis

| | Temp. regime 13/10°C | | | | | | | Temp. regime 19/16°C | | | | | | |
| | Females | | | | Males | | | Females | | | | Males | | |
Month	Weight (g)	GSI	ΔS	Stage	Weight (g)	GSI	ΔS	Weight (g)	GSI	ΔS	Stage	Weight (g)	GSI	ΔS
Jul.	117.9				120.9			299.0				281.0		
Aug.	150.5	0.2	33.0	PV	153.0	0.3	32.6	425.8	0.2	127.5	PV	383.1	0.4	103.6
Oct.	199.2	0.3	49.3	PV	203.8	0.2	51.3	665.6	0.5	243.1	PV	561.8	0.3	180.2
Dec.	294.4	0.8	97.5	PV	282.3	0.3	79.2	971.4	1.3	318.2	PV	788.1	0.3	228.5
Feb.	344.7	0.7	52.8	PV	337.8	0.7	57.8	1179.8	1.6	227.2	EV	893.4	0.4	108.6
Apr.	440.3	1.7	103.2	EV	396.9	0.5	60.9	1534.7	2.3	389.7	EV	1099.0	0.9	209.7
Jun.	510.2	1.9	79.8	EV	446.3	0.4	51.1	1537.5	7.3	114.3	LV	1075.9	0.9	−13.3
Aug.	595.2	1.6	94.7	EV	486.1	0.3	41.0	1265.2	3.2	−231.5	LV	907.2	0.4	−165.3

growing conditions compared with wild conditions, the fish may reach this size threshold at an earlier age. This would lead to a decrease of the age at first maturity, which is in accordance with our findings. After reaching the threshold size for onset of maturation, the positive relationship between fecundity and body size (Wootton 1979) will favour rapid growth in females (Roff 1982), whereas no such relationship exists for males. Roff (1983) hypothesized that growth decrease in males was a survival strategy, as it is of greater survival value for the males to forage relatively little, i.e. to feed and grow less, as foraging may expose the fish to increased risk of predation. In females the reproductive output increases with body size (Wootton 1979), which can compensate for the increased predation risk (Roff 1982, 1983; Rijnsdorp & Ibelings 1989).

In salmonids it is suggested that differences in growth seen between maturing and non-maturing fish may be caused by hormonally induced differences in feeding behaviour and foraging strategy (Metcalfe, Huntingford & Thorpe 1986; Rowe & Thorpe 1990). Further, Taranger (1993) suggested that the increase in growth rate of maturing Atlantic salmon occurred concomitant with, or after, the first endocrine signs of sexual maturation. Hence, the growth enhancement seen in maturing salmonids (Nævdal et al. 1979; McLay, Youngson, Wright & Johnstone 1992) is a consequence of sexual maturation rather than a

cue triggering or enabling maturation. It has been hypothesized that size differences between maturing and non-maturing fish could be traced back to the year before maturation (Rowe & Thorpe 1990). In their study with rainbow trout, Nævdal et al. (1979) found that the increased size of maturing fish could be traced back to the summer of the previous year.

Similar growth differences between maturing and non-maturing fish have been seen in some studies with flatfish. Rijnsdorp (1993) indicated that maturation of female plaice was highly correlated with growth rate in the last completed year. He further suggested that growth rate 3 years prior to sampling influenced maturation of plaice. The present study clearly demonstrates that size and growth differences between maturing and non-maturing turbot could be traced back as early as February 1992 (age 8 months, Figs 1 and 2), which is approximately 16 months before first spawning (Devauchelle et al. 1988). By October 1992 (age 15 months, Fig. 3f), maturing females and maturing males were generally the largest fish (> 600 g), consequently size grading is recommended in the fall prior to expected maturation to remove most of the non-maturing (slower-growing) fish.

Further, the total energy invested in growth and reproduction, i.e. the surplus energy (Δ*S*), was similar in males and females in early fall 1992, but diverged thereafter as Δ*S* in males levelled off whereas female Δ*S* continued to increase. It appears that males switch from maximum growth to reduced

Table 4 Comparison of size relationship (wet weight) between males and females of some species of flatfish. A comparison of the size relationship between the sexes of wild and hatchery-reared fish of same species is made when data are available

Scientific name	Common name	Male size[1]	Age (years)	Origin of fish[2]	Data source
BOTHIDAE					
Scophthalmus rhombus (L.)	Brill	72	3.0	W	Robert & Vianet (1988)
Scophthalmus maximus (Rafinesque)	Turbot	86	5.0	W	Déniel (1990)
		96	2.5	W	Déniel (1990)
		67	2.5	HR	Devauchelle *et al.* (1988)
		74	2.0	HR	This paper (all groups combined)
PLEURONECTIDAE					
Glyptocephalus cynoglossus (L.)	Witch flounder	102	3.0	W	Bowering (1976)
Hippoglossus hippoglossus (L.)	Atlantic halibut	73	6.0	W	Jákupsstovu & Haug (1988)
		62	6.0	W/HR	Björnsson (1995)
		38	30.0	W	Devold (1938)
Limanda limanda L.	Dab	94	2.0	W	Lozán (1992)
Liopsetta putnami (Gill)	Smooth flounder	88	3.0	W	Armstrong & Starr (1994)
Platichthys flesus (L.)	Flounder	93	3.0	W	Berner & Sager (1985)
Pleuronectes platessa L.	Plaice	88	2.0	W	Rijnsdorp & Ibelings (1989)
Pseudopleuronectes americanus Walbaum	Winter flounder	88	3.0	W	Vaillancourt, Brêthes & Desrosiers (1985)
PSETTODIDAE					
Psettodes erumei (Schneider)	Queensland halibut	95	3.0	W	Druzhinin & Petrova (1980)
SOLEIDAE					
Solea solea Quensel	Sole	62	8.0	W	De Veen (1976)
		49	8.0	HR	Houghton, Last & Bromley (1985)

[1]Male size is given as % of female weight at same age.

[2]Origin of fish: W, wild; HR, hatchery reared; W/WR, collected from wild and reared under culture conditions.

growth around 900 g (Fig. 1). A similar growth shift in males was reported by Rijnsdorp & Ibelings (1989) in their study with plaice. The growth decrease observed in male turbot cannot be explained on the basis of energy allocation to the gonads, as this is much smaller than for females (Table 3). In general, flatfish spend less energy on metabolism and convert relatively more energy into growth (Fonds, Cronie, Vethaak & van der Puyl 1992) than roundfish. As there is no indication in the literature of a higher metabolism of male flatfish in relation to females, it is suggested that the shift in surplus energy in males seen in earlier studies on flatfish (Roff 1983; Rijnsdorp 1989; Rijnsdorp & Ibelings 1989) and in the present study is mainly an energy-saving mechanism. In support of this hypothesis, a survey of available literature on the size relationship between male and female flatfish is presented (Table 4). Available data (Table 4) show that males are nearly always smaller than females, apparently before the onset of maturation [turbot,

Devauchelle *et al.* (1988); brill, Robert & Vianet (1988); plaice, Rijnsdorp & Ibelings (1989); dab, Lozán (1992)]. After maturation the sexes diverge in growth pattern as size differences become larger with age [Atlantic halibut, Devold (1938); sole, De Veen (1976); turbot, Déniel (1990)]. In all these species the relative gonad production (*GSI*) is lower in males than females. In conclusion, the energy spent by males in growth and reproduction (Fig. 1, Tables 3 and 4) is less than by females, indicating some energy-saving mechanism in males. Reduced food intake of males (Lozán 1992) compared with females, and thus less available energy for growth and reproduction in males, lends some support to the above hypothesis. Further, the study of Rijnsdorp & Ibelings (1989) showed that mature males use less energy in their metabolism than do mature females. They reported a higher metabolic rate in female plaice during the spawning season than in males (9.1 kJf day^{-1} versus 7.3 kJf day^{-1}, respectively where kJf is the physiological useful energy).

Gonadosomatic index can be interpreted as a rough estimate of the reproductive effort made by the fish (Moyle & Cech 1982). Although teleost females generally have higher gonadal investment than males (Craig 1977; Vøllestad & Jonsson 1988; Rijnsdorp 1989; present study), these differences may partly be evened out by the greater investment by males in reproductive structure and in reproductive behaviour. Where eggs are guarded by one sex, the guarding sex (often the male) is the larger fish [Cyprinidae, Scott & Crossman (1973); Cichlidae, Lowe-McConnell (1987)], as there may be advantages in being large when parental care is involved, i.e. larger males may be better able to drive off predators of their eggs and young (Moyle & Cech 1982). Roff (1983) demonstrated [using data of Scott & Crossman (1973) on freshwater fishes of North America] a clear association between the relative size of the males and their reproductive behaviour. In species where males displayed territorial or parental behaviour they were larger than the females, and vice versa in species with no territorial or parental behaviour.

A negative correlation between average *GSI* and specific growth rate was found for both males and females (Fig. 4), indicating that the process of growth and maturation are to some degree mutually exclusive in turbot. Aerobic activities of a fish are restricted by the maximum level of metabolism [metabolic scope; Priede (1985)]. If maturation and spawning in turbot fill a substantial part of the metabolic scope of the maturing fish, i.e. high *GSI*, the oxygen supply for other activities including digestion and somatic growth might be restricted. Accordingly, a high reproductive effort (measured as high *GSI*) would indicate that growth potential is diverted to gonad tissue, hence these processes would be negatively correlated, as seen in the present study (Fig. 4).

It appears that relative size differences between males and females are greater under culture conditions compared with fish taken from the wild (Table 4), and that these differences are evident earlier in culture (present study Fig. 1) than at sea (Devauchelle *et al.* 1988). Part of this difference could be due to reduced age at first maturity in culture, as growth of the sexes diverges after the onset of maturing (Bowering 1976; Rijnsdorp 1989; Rijnsdorp & Ibelings 1989; present study). Jones (1974) studied sexual maturity in turbot and reported the age of 50% maturation to be 4.5 years. Déniel (1990) determined the age of first maturity

in turbot to be 4.0 years. In contrast, in the present study, 43% and 50% of the fish reared at 19/16°C and 16/16°C respectively were sexually mature at the age of 2 years. Another explanation could be related to better feeding conditions (Houghton *et al.* 1985) of the fish in culture, as feed is available at all times. In the wild, however, this may not be possible as fish migrate to spawning areas which can be separated from preferred feeding areas (Harden Jones 1966). Further, genetic differences in feeding behaviour (Lozán 1992) may favour growth in females under conditions where the fish are always fed *ad libitum*.

Differences in maturing proportions between the different temperature regimes were noted, as a higher proportion of the fish reared at 19/16°C and 16/16°C matured than at 13/10°C and 10/10°C (43.9% vs. 16.1%, respectively). This indicates a large phenotypic plasticity for the onset of maturation in turbot, and that environmental manipulations during the juvenile stage an affect the onset of maturation. This observation could help to explain the observed reduction in age at first maturity seen in wild stocks of flatfish [sole, De Veen (1976); plaice, Rijnsdorp (1989); witch flounder, Bowering & Brodie (1991)] as these changes coincide with higher juvenile growth of these species in the same period (Bowering & Brodie 1991; Rijnsdorp & van Beek 1991). No differences in maturity proportion between males and females at the age of 2 years were found in the present study (Table 2, $P > 0.09$). In contrast, earlier studies on other flatfish species have reported that males mature at a younger age than females (Bowering 1976; Druzhinin & Petrova 1980; Jákupsstovu & Haug 1988; Armstrong & Starr 1994). This discrepancy might be explained by the fact that females in the present study matured at younger age than observed in the wild (Jones 1974; Devauchelle *et al.* 1988; Déniel 1990), whereas the males did not, so that no sexual differences in maturity proportions at the age of 2 years could be detected. The biological material used in the present study had a narrow genetic base (offspring of two males and one female). The disadvantage of using such material is that it is not representative of the total variation found in that species (Falconer 1989), whereas the advantage of using groups with similar genetic background is that the effects of specific factors affecting processes in the fish are easier to study (Falconer 1989).

Conclusions

Turbot males grew less than females from 8 months post hatch (Figs 1 and 2). Significant growth differences between maturing and non-maturing fish (GCM MANOVA) occurred from the age of 9 months post hatch (Fig. 2), indicating a correlation between maturation and growth rate. Maturing females had the highest growth and reached the largest average size of all groups (1.8 kg in 20 months). As turbot is currently marketed at a weight approaching 2 kg (Campos Piñon 1994), and male body weight levelled off around 900–1100 g (Fig. 1), methods should be developed to achieve all-female broods.

Acknowledgments

References

Alm G. (1959) Connection between maturity, size, and age in fishes. *Meddelanden från statens undersökings-och försöksanstalt för sötvattfisket* **40**, 5–145.

Armstrong M.P. & Starr B.A. (1994) Reproductive biology of the Smooth flounder in Great Bay estuary, New Hampshire. *Transactions of the American Fisheries Society* **123**, 112–114.

Bagenal T.B. (1966) A short review of fish fecundity. In: *The Biological Basis of Freshwater Fish Production* (ed. by S.D. Gerking), pp. 89–111. Blackwell Scientific Publications, Oxford.

Bergstad O.A. (1990) Distribution, population structure, growth and reproduction of the roundnose grenadier *Coryphaenoides rupestris* (Pisces: Macrouridae) in the deep waters of the Skagerrak. *Marine Biology* **107**, 25–39.

Berner M. & Sager G. (1985) Untersuchungen zu Längen- und Massewachstum, Zuwchs und Längen/Masse-Relation der Geschlechter der Flunder (*Platichthys flesus* L.) in der Bornholmsee nach Datenreihen von Berner. *Fischerei-Forschung Wissenschaftliche Schriftenreihe* **23**, 36–42.

Björnsson B. (1995) The growth pattern and sexual maturation of Atlantic halibut (*Hippoglossus hippoglossus*

L.) reared in large tanks for 3 years. *Aquaculture* **138**, 281–296.

Bowering W.R. (1976) Distribution, age and growth, and sexual maturity of witch flounder (*Glyptocephalus cynoglossus*) in Newfoundland waters. *Journal of the Fisheries Research Board of Canada* **33**, 1574–1584.

Bowering W.R. & Brodie W.B. (1991) Distribution of commercial flatfishes in the Newfoundland–Labrador region of the Canadian Northwest Atlantic and changes in certain biological parameters since exploitation. *Netherlands Journal of Search Research* **27**, 407–422.

Burton M.P. & Idler D.R. (1984) The reproductive cycle in winter flounder *Pseudopleuronectes americanus* (Walbaum). *Canadian Journal of Zoology* **62**, 2563–2567.

Campos Piñon G. (1994) Penetration and marketing of cultured turbot in restaurants. In: *Turbot Culture: Problems and Prospects* (ed. by P. Lavens & R.A.M. Remmerswaal), pp. 214–215. European Aquaculture Society, Oostende, Belgium.

Chambers R.C. & Miller T.J. (1995) Evaluating fish growth by means of otolith increment analysis: special properties of individual-level longitudinal data. In: *Recent Developments in Fish Otolith Research* (ed. by D.H. Secor, J.M. Dean & S.E. Campana), pp. 155–175. University of South Carolina Press, Columbia, SC.

Charlesworth B. & León J.A. (1976) The relation of reproductive effort to age. *The American Naturalist* **110**, 449–459.

Craig J.F. (1977) The body composition of adult perch, *Perca fluviatilis* in Windermere, with reference to seasonal changes and reproduction. *Journal of Animal Ecology* **46**, 617–632.

Déniel C. (1984) La reproduction des poissons plats (Téléostéens, Pleuronectiformes) en baie de Douarnenez. II. Cycles sexuels et fécondité des Soleidae: *Solea vulgaris vulgaris, S. lascaris, Buglossidium luteum* et *Microchirus variegatus. Cahiers de Biologie Marine* **XXV**, 257–285.

Déniel C. (1990) Comparative study of growth of flatfishes on the west coast of Brittany. *Journal of Fish Biology* **37**, 149–166.

Devauchelle N., Alexandre J.C., LeCorre N. & Letty Y. (1988) Spawning of turbot (*Scophthalmus maximus*) in captivity. *Aquaculture* **69**, 159–184.

De Veen J.F. (1976) On changes in some biological parameters in the North Sea sole (*Solea solea* L.). *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **37**, 60–90.

Devold F. (1938) The North Atlantic halibut and net fishing. *Fiskeridirektoratets Skrifter serie Havundersøkelser* **5**, 5–47.

Dorn M.W. (1992) Detecting environmental covariates of Pacific whiting *Merluccius productus* growth using a growth-increment regression model. *Fishery Bulletin, US* **90**, 260–275.

Druzhinin A.D. & Petrova Ye.G. (1980) Some data on the ecology and growth of *Psettodes erumei* (Family

Psettodidae Order Pleuronectiformes) of the Gulf of Aden. *Journal of Ichthyology* **20,** 143–147.

Elvinson P. & Johansson K. (1993) Genetic and environmental components of variation in body traits of rainbow trout (*Oncorhynchus mykiss*) in relation to age. *Aquaculture* **118,** 191–204.

Falconer D.S. (1989) *Introduction to Quantitative Genetics* (3rd edition). John Wiley & Sons, New York, 438 pp.

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

Harden Jones F.R. (1966) *Fish Migration*. Edward Arnold, London, 325 pp.

Houde E.D. & Schekter R.C. (1981) Growth rates, rations and cohort consumption of marine fish larvae in relation to prey concentrations. *Rapports et Procès-verbaux des Réunions, Conseil International pour l'Exploration de la Mer* **178,** 441–453.

Houghton R.G., Last J.M. & Bromley P.J. (1985) Fecundity and egg size of sole (*Solea solea* (L.)) spawning in captivity. *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **42,** 162–165.

Imsland A.K., Folkvord A. & Stefansson S.O. (1995) Growth, oxygen consumption and activity of juvenile turbot (*Scophthalmus maximus*) reared under different temperatures and photoperiods. *Netherlands Journal of Sea Research* **34,** 149–159.

Jákupsstovu S.H.í. & Haug T. (1988) Growth, sexual maturation and spawning seasons of Atlantic halibut, *Hippoglossus hippoglossus*, in Faroese waters. *Fisheries Research* **6,** 201–215.

Jones A. (1974) Sexual maturity, fecundity and growth of the turbot *Scophthalmus maximus* L. *Journal of the Marine Biological Association of the United Kingdom* **54,** 109–125.

Lavens P. & Remmerswaal R.A.M. (eds) (1994) *Turbot Culture: Problems and Prospects*. European Aquaculture Society, Oostende, Belgium, 358 pp.

Lowe-McConnell R.H. (1987) *Ecological Studies in Tropical Fish Communities*. Cambridge University Press, Cambridge, 382 pp.

Lozán J.L. (1992) Sexual differences in food intake, digestive tract size, and growth performance of the dab, *Limanda limanda* L. *Netherlands Journal of Sea Research* **29,** 223–227.

McLay H.A., Youngson A.F., Wright R.S. & Johnstone R. (1992) Effects of rearing density on sexual maturation and growth in sea-cage reared Atlantic salmon, *Salmo salar* L. *Aquaculture and Fisheries Management* **23,** 353–365.

Metcalfe N.B., Huntingford F.A. & Thorpe J.E. (1986) Seasonal changes in feeding motivation of juvenile Atlantic salmon (*Salmo salar*). *Canadian Journal of Zoology* **64,** 2439–2446.

Miller J.M., Burke J.S. & Fitzhugh G.R. (1991) Early life history of Atlantic North American flatfish: likely (and unlikely) factors controlling recruitment. *Netherlands Journal of Sea Research* **27,** 261–275.

Moyle P.B. & Cech J.J. (1982) *Fishes: An Introduction to Ichthyology*. Prentice–Hall, Englewood Cliffs, NJ, 593 pp.

Nævdal G., Holm M., Lerøy R. & Møller D. (1979) Individual growth rate and age at sexual maturity in rainbow trout. *Fiskeridirektoratets Skrifter serie Havundersøkelser* **17,** 1–10.

Nævdal G., Lerøy R. & Møller D. (1983) Sources of variation in weight and length of Atlantic salmon. *Fiskeridirektoratets Skrifter serie Havundersøkelser* **17,** 359–366.

Nijhof M. (1994) Research on nutrition and growth in the culture of post larval turbot (*Scophthalmus maximus* L.). In: *Turbot Culture: Problems and Prospects* (ed. by P. Lavens & R.A.M. Remmerswaal), pp. 137–165. European Aquaculture Society, Oostende, Belgium.

Panfili J., Ximénès M.-C. & Crivelli A.J. (1993) Sources of variation in growth of the European eel (*Anguilla anguilla*) estimated from otoliths. *Canadian Journal of Fisheries and Aquatic Sciences* **51,** 506–515.

Peterson R.G., Winkelman A., Devlin R. & Harrower W. (1992) The effect of sex on growth of Chinook salmon. *Bulletin of the Aquaculture Association of Canada* **92**(3), 37–39.

Prentice E.F., Park D.L., Flagg T.A. & McCutcheon S. (1985) A study to determine the biological feasibility of a new fish tagging system, 1985–1986. Dept of Commerce, NOAA, NMFS, Northwest and Alaska Fisheries Center, Seattle, WA, 89 pp.

Priede I.G. (1985) Metabolic scope in fishes. In: *Fish Energetics* (ed. by P. Tytler & P. Calow), pp. 33–64. Croom Helm, London.

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

Rijnsdorp A.D. (1989) Maturation of male and female North Sea plaice (*Pleuronectes platessa* L.). *Journal du Conseil, Conseil International pour l'Exploration de la Mer* **46,** 35–51.

Rijnsdorp A.D. (1993) Relationship between juvenile growth and the onset of sexual maturity of female North Sea plaice, *Pleuronectes platessa*. *Canadian Journal of Fisheries and Aquatic Sciences* **50,** 1617–1631.

Rijnsdorp A.D. & Ibelings B. (1989) Sexual dimorphism in the energetics of reproduction and growth of North Sea plaice, *Pleuronectes platessa* L. *Journal of Fish Biology* **35,** 401–415.

Rijnsdorp A.D. & van Beek F.A. (1991) Changes in growth of plaice *Pleuronectes platessa* L. and sole *Solea solea* (L.) in the North Sea. *Netherlands Journal of Sea Research* **27,** 441–457.

Robert F. & Vianet R. (1988) Age and growth of *Psetta maxima* (Linné, 1758) and *Scophthalmus rhombus* (Linné, 1758) in the Gulf of Lion (Mediterranean). *Journal of Applied Ichthyology* **4,** 111–120.

Roff D.A. (1982) Reproductive strategies in flatfish: a first synthesis. *Canadian Journal of Fisheries and Aquatic Sciences* **39,** 1686–1698.

Roff D.A. (1983) An allocation model of growth and reproduction in fish. *Canadian Journal of Fisheries and Aquatic Sciences* **40,** 1395–1404.

Roff D.A. (1991) The evolution of life-history variation in fishes, with particular reference to flatfishes. *Netherlands Journal of Sea Research* **27,** 197–207.

Rosenberg A.A. & Haugen A.S. (1982) Individual growth and size-selective mortality of larval turbot (*Scophthalmus maximus*) reared in enclosures. *Marine Biology* **72,** 73–77.

Rowe D.K. & Thorpe J.E. (1990) Differences in growth between maturing and nonmaturing male Atlantic salmon (*Salmo salar* L.) parr. *Journal of Fish Biology* **36,** 643–658.

Samuel M. (1986) Spawning of *Nemipterus japonicus* (Bassi) in Kuwait's waters and growth differences by sex. *Kuwait Institute of Scientific Research. Annual Research Report* (1986), 15–17.

Scott W.B. & Crossman E.J. (1973) Freshwater fishes of Canada. *Bulletin of the Fisheries Research Board of Canada* **184,** 966 pp.

Soengas J.L., Barciela P. & Aldegunde M. (1995) Variations in carbohydrate metabolism during gonad maturation in female turbot (*Scophthalmus maximus*). *Marine Biology* **123,** 11–18.

Sokal R.R. & Rohlf R.J. (1995) *Biometry* (3rd edition). Freeman, San Francisco, 887 pp.

Stearns S.C. (1992) *The Evolution of Life Histories*. Oxford University Press, Oxford, 249 pp.

Stephens M.A. (1974) EDF statistics for goodness of fit and some comparisons. *Journal of the American Statistical Association* **69,** 730–737.

Taranger G.L. (1993) *Sexual maturation in Atlantic salmon, Salmo salar L.; aspects of environmental and hormonal control.* Dr Scient. Thesis. University of Bergen, Norway.

Timm N.H. (1980) Multivariate analysis of variance of repeated measurements. In: *Handbook of Statistics* (ed. by P.R. Krishnaiah), Vol. 1, pp. 41–87. Analysis of variance. North-Holland Publishing Company, Amsterdam, Netherlands.

Vaillancourt F., Brêthes J.-C.F. & Desrosiers G. (1985) Croissance de la plie rouge (*Pseudopleuronectes americanus*) de l'estuaire maritime du Saint-Laurent. *Canadian Journal of Zoology* **63,** 1610–1616.

Vøllestad L.A. & Johnsson B. (1988) A 13-year study of the population dynamics and growth of the European eel *Anguilla anguilla* in a Norwegian river: evidence for density-dependent mortality, and development of a model for predicting yield. *Journal of Animal Ecology* **57,** 983–997.

Ware D.M. (1978) Bioenergetics of pelagic fish: theoretical change in swimming speed in relation to body size. *Journal of the Fisheries Research Board of Canada* **35,** 220–228.

Ware D.M. (1980) Bioenergetics of stock and recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* **37,** 1012–1024.

Wootton R.J. (1979) Energy cost of egg production and environmental determinants of fecundity in teleost fishes. *Symposia of the Zoology Society of London* **44,**133–159.

Zar J.H. (1984) *Biostatistical Analysis* (2nd edition). Prentice–Hall, Englewood Cliffs, NJ, 718 pp.