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Long photoperiod delayed spawning and increased somatic growth in gilthead seabream (*Sparus aurata*)

George Wm. Kissil [a,*], Ingrid Lupatsch [a], Abigail Elizur [a], Yonathan Zohar [b]

[a] *Israel Oceanographic and Limnological Research, National Center for Mariculture, P.O. Box 1212, Eilat 88112, Israel*

[b] *Center of Marine Biotechnology, University of Maryland Biotechnology Institute, 701 E Pratt St, Baltimore, MD 21202, USA*

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Abstract

The effects of extended photoperiods, mimicking the longest day of the year, were studied in 1- and 2-year seabream. The photoperiod regimes started in late July, 36 and 39 days after the summer solstice and continued for 11 months, well beyond the natural reproductive season of December–March. Regime 1 (long day, 15.5L:8.5D), which used natural and fluorescent light, reduced the incidence of maturity in both year classes and females did not spawn although some gonadal development was observed. Among all 1-year sampled fish of regime 1, a maximum of 5% became spermiating males (March) and 5% reached the yolk granule stage of vitellogenesis (VO3; 250–400 μm diameter) by May. Among 2-year sampled fish of regime 1, 45% became spermiating males and 25% were females, which reached the advanced vitellogenesis stage (VO4; 400–600 μm) by April. Regime 2 (skeleton photoperiod), consisting of natural light and a 1.5-h pulse of fluorescent light during the period 14–15.5 h after sunrise, postponed gonadal development and spawning for up to 3 months. In this regime, a maximum of 80% of 1-year sampled fish were spermiating males in February and a maximum of 10% were VO3 stage females in March. In the sampled 2-year fish, the maximum levels were 50% spermiating males in February and 25% VO3 stage females in March. Control fish, which were exposed to the natural photoperiod (29°34′N), spawned during their natural season. The maximum levels for 1-year sampled control fish were 95% spermiating males and no females in December, while among 2-year sampled fish, maxima of 75% males in February and 45% VO4 stage females in November. Final average

* Corresponding author. Fax: +972-8-637-5761.

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weights of photoperiod treated fish (1-year = 430 g—regime 1, 400 g—regime 2; 2-year = 582 g —regime 1, 518 g—regime 2) were significantly greater ($p < 0.05$) than control fish (1-year = 341 g; 2-year = 476 g). Daily feed consumption (g/100 g fish) dropped from an average of 1.83 to 0.93 g for 1-year fish during August–December and from 0.88 to 0.54 g for 2-year fish during the same period. This was correlated with reduced autumn and winter water temperatures (26–20°C summer to winter change) and increased fish weight in all treatments. Daily feed consumption was also affected by the onset of spawning in the control and regime 2 (skeleton photoperiod) treatments of both 1- and 2-year fish. The efficiency of feed utilization (FCR) and protein and energy retention were all affected by the photoperiod regimes and followed the same pattern of decrease as weight gain, regime 1 (long day) > regime 2 (skeleton photoperiod) > control. © 2001 Elsevier Science B.V. All rights reserved.

Keywords: Photoperiod control; Sexual maturation; Spawning; Growth

1. Introduction

Gilthead seabream begin gonadal development during September in preparation for winter spawning which starts around late December to early January in the eastern Mediterranean region. Spawning or gamete release occurs over a 3–4-month period, during which females can spawn 0.5–2 times their body weight in eggs (Zohar et al., 1995) through multiple spawnings. The majority of nutrients required to produce this large volume of eggs are derived from the food consumed supplemented by nutrients from body reserves, as indicated by changes in the body composition (Harel et al., 1994). Reproduction of seabream causes a loss in body weight, which takes a number of months to replenish after spawning ceases. The net result is a 3–4-month spawning period, during which females lose weight and males undergo a reduced weight gain while continuing to feed.

Photoperiod manipulation has been used successfully to hasten growth, development and survival of young stages in a number of fish, gilthead seabream (Tandler and Helps, 1985; Silva-Garcia, 1996), European sea bass, *Dicentrarchus labrax* (Barahona, 1979), and barramundi, *Lates calcarifer* (Barlow et al., 1995). In addition, modified photoperiod regimes have also been successfully used to alter the rate of sexual maturation and time of spawning of the commercially important European sea bass (Carrillo et al., 1995), gilthead seabream (Zohar et al., 1995), rainbow trout (*Oncorhynchus mykiss*), brown trout (*Salmo trutta*), and Atlantic salmon (*Salmo salar*) (Bromage, 1995). The main objective is to extend the spawning period for greater availability of stockable fry. In contrast, a long day photoperiod (15L:9D) in European sea bass and continuous light in Atlantic cod (*Gadus morhua* L.) have been used to delay or stop sexual maturation or spawning and enhance growth (Carrillo et al., 1989; Karlsen et al., 1999).

There are a number of examples among salmonids of delayed maturation and spawning, with a resultant gain in growth, due to photoperiod control. Atlantic salmon post smolts showed increased growth and a drop from 23.5% to 10% of maturing fish, which have reduced flesh quality as a result of 4 months of continuous light in addition to the natural daylight (Taranger et al., 1995). Bromage et al. (1984) delayed spawning of rainbow trout 12–14 weeks beyond their natural winter spawning using constant short

days (6L:18D), and in a separate trial with this same photoperiod, demonstrated they grew better on the same feed ration as constant (24L:0D) or long day (18L:6D) treated fish. Duston and Bromage (1986) similarly reported postponement in spawning in rainbow trout with delays of up to 5 months but no information was given on relative growth of these fish.

Photoperiod control of gonadal maturation can also be used to delay or prevent development of eggs and sperm in order to save the energy reserves used by the fish in this process. Kadmon et al. (1985a,b) showed that the winter spawning weight loss of cultured gilthead seabream could be arrested through the use of photoperiod control. Groups of seabream maintained under a constant 16L:8D photoperiod demonstrated a relatively constant weight gain during winter as compared with fish maintained under natural conditions, and their sexual differentiation was inhibited.

The potential use of photoperiod control to delay or postpone gonadal development and reproduction in commercial seabream culture, thereby increasing overall weight gain and allowing for storage of market size fish over the winter without weight loss, has obvious economic benefits. However, before putting photoperiod control into use as a commercial management practice, it is important to evaluate different ways of maintaining a long-day photoperiod. The objectives of this study were: (a) to determine the effectiveness of different photoperiod regimes in postponing gonadal development and reproduction, thus, preventing fish weight loss, and (b) to evaluate the photoperiod effects on feed utilization. Two different photoperiod regimes, both incorporating natural and fluorescent light, were used in this study: (a) constant long day (regime 1), and (b) a long day interrupted by a dark period or "skeleton photoperiod" (regime 2) (Goldman and Elliott, 1981). The "skeleton photoperiod" concept has been used in early plant and animal studies to determine the mechanism underlying photoperiodic time measurement. Short duration of light (pulses) were shown to initiate or inhibit seasonal processes, such as reproduction, if they coincided with the photoinducible or photosuppressive phase, respectively, of an endogenous circadian cycle of photosensitivity (Follett, 1978; Turek and Campbell, 1979; Goldman and Elliott, 1981). The "skeleton photoperiod" in this experiment tested the assumption that fish would respond in the same way as they do to a constant long day and not translate a dark period as a signal of shortening of the day. If this assumption proved true, then it would provide a possible method to reduce the cost of maintaining a long day photoperiod. This experiment also compared the effect of photoperiod control on 1-year (mainly males) and 2-year (mixed sexes) maturing seabream.

2. Materials and methods

2.1. Fish and holding conditions

Two separate trials were run using seabream obtained from a local commercial farm. In each trial, fish were size graded and stocked into a six-tank (4000 l each) seawater system equipped with photoperiod control and shaded from direct sunlight by an overhead roof. Trial 1, started on July 29, 1992 with second year fish of 315-g average

weight, stocked 110 fish/tank. Trial 2, initiated on August 1, 1993 using first year fish of 65-g average weight, stocked at 120 fish/tank. Fish were fed locally produced pelleted commercial seabream diets (Matmor, Mobile Post Evtach, Israel; Table 1) twice daily to satiation, making sure no food was left uneaten, and daily feed consumption was recorded. The composition of the feeds changed between trials 1 and 2 due to improvements made in the formulation at the feed mill. All tanks were aerated and ambient temperature seawater (20–26°C annual range) flowed into them at a rate of 25 l/min, providing nine complete water exchanges every 24 h.

2.2. Experimental treatments

Light tight covers were fitted on four of the tanks so that the two different photoperiod regimes, which were implemented from the time of stocking fish in the tanks, could be tested in duplicate. The two remaining tanks had no covers and served as controls with the natural photoperiod at latitude 29°34′N. Tank covers incorporated a 36-W fluorescent daylight bulb (Mazdafluor, France), located 20 cm above the water surface when the covers were closed, which provided approximately 800 lux at the water's surface. The fluorescent lights were automatically activated by an electric time clock without providing dawn or twilight periods.

Covers were routinely opened before sunrise and closed immediately after sunset so that natural daylight was part of the photoperiod regimes. Regime 1 (long day) provided 15.5 h of continuous light daily by combining natural and fluorescent light. Fluorescent lights were turned on 1 h before sunset while the tank covers were still open above the tanks to prevent a dark period during the 15.5 h. Regime 2 (skeleton photoperiod) gave only an additional 1.5-h pulse of fluorescent light beyond the natural daylight period. The pulse was provided in such a manner that 15.5 h elapsed between sunrise and the end of the 1.5-h pulse. At 29°34′N latitude, the period of darkness between sunset and the start of the 1.5-h pulse ranged from 0–76 min during July 1–August 31 to a maximum of 225 min by December 21. Natural light ranged from a minimum intensity of 6 lux to a maximum of 1300 lux at the water's surface between sunrise and sunset.

2.3. Parameters monitored

In both trials, monthly weighing of all experimental fish in groups of 10 individuals was carried out to determine weight gain and feed utilization. In parallel, samples of fish from each tank ($n = 10$) underwent gonadal biopsy (according to Zohar and Gordin, 1978) to determine their sex and stage of development. Gonadal tissue was examined

Table 1
Proximate composition of commercial feed used in these trials (g/kg as fed)

	Dry matter	Crude protein	Lipid	Ash	Gross energy (MJ/kg)
Trial 1 (2-year fish)	931	398	99	80	18.67
Trial 2 (1-year fish)	925	460	130	125	19.54

microscopically to determine oocyte diameter and observe other parameters used to define the stage of ovarian development of the fish. No attempt was made to classify males beyond spermiating stage as this would require sacrificing them and removal from the experiment. Fish in which the sex was not clear microscopically were considered to be in the previtellogenesis (PV) stage.

Gonadal development was defined using the following criteria (Zohar and Gordin, 1979; Zohar et al., 1984; Wallace and Selman, 1981; Tyler and Sumpter, 1996):

PV = Previtellogenesis oocytes at 90–130 μm diameter—sex unknown (immature bisexual seabream gonads contain previtellogenesis oocytes).
V01 = Vitellogenesis 1, the cortical alveoli stage: oocytes are 110–140 μm in diameter, only carbohydrate globules are present in the ooplasm, which are the future cortical alveoli.
V02 = Vitellogenesis 2, the lipid vesicle stage: oocytes are 130–250 μm in diameter, lipid vesicles are formed surrounding the nucleus, cortical alveoli multiply in number.
V03 = Vitellogenesis 3, yolk granule stage: oocytes are 250–400 μm in diameter, proteinaceous yolk granules start to appear in the ooplasm periphery and spread towards its center.
V04 = Vitellogenesis 4, advanced vitellogenesis stage: oocytes are 400–600 μm in diameter, yolk granules multiply in number, enlarge in size and occupy most of the ooplasm. Cortical alveoli are displaced to the oocyte periphery and lipid vesicles and droplets converge in the middle of the oocyte.

Determining sex ratio from the gonadal biopsies in these experimental groups was complicated by the fact that *Sparus aurata* is a protandrous hermaphrodite (Zohar et al., 1978) and in a few cases, both sperm and oocytes in various developmental stages were detected in the same fish. These cases were not included in the sex ratio data.

The time of gamete release or spawning was determined according to a number of factors: courting behavior, the presence of thick foam covering the surface of the holding tanks thought to be from the release of gametes, the presence of ovulated eggs and sperm in biopsied fish, reduced feeding and the dramatic decrease in weight found in periodic weighings.

2.4. Analyses

Determination of gonadosomatic index (GSI) and analysis of proximate body composition along with the subsequent calculations of productive protein value (PPV) and energy retention value (ERV), were carried out only for 2-year fish. All other analyses were performed on both 1- and 2-year fish.

For the 2-year fish (Trial 1), 10 fish were sampled initially, then subsequent samples of five fish from each tank were taken on March 26, 1993 and on June 2, 1993. The initial and March samples were examined to determine the gonadosomatic index and then frozen for further analyses.

$$\mathrm{GSI} = (\text{weight of gonads} / \text{weight of fish}) \times 100$$

Proximate body composition of the 2-year fish was determined using the frozen initial and June samples. For these analyses, frozen samples were ground twice using a commercial meat grinder (3-mm die), a sample removed for dry matter determination and the remaining samples freeze-dried. The freeze-dried samples were then broken up in a blender for homogeneity before the remaining analyses were performed.

Feed samples for proximate analysis were prepared by grinding them in a hammer-mill equipped with a 1-mm-sieve screen. Dry matter in all samples (feed and fish) was calculated from the weight loss after 24 h of drying at 105°C. All samples both freeze-dried and frozen were analyzed for dry matter content so moisture corrections could be made for the remaining analyses. Crude protein was measured using the standard Kjeldahl technique and by multiplying N by 6.25. Crude lipid was determined using a chloroform–methanol extraction procedure (Folch et al., 1957). Samples were mixed using a high-speed homogenizer for 5 min and the lipid measured gravimetrically after separation and vacuum drying. Ash content was calculated from weight loss after incineration of samples for 24 h at 550°C. Gross energy content of samples was determined through combustion in a Parr bomb calorimeter using benzoic acid as the standard.

Feed conversion ratio and protein and energy accumulation in fish tissues were calculated using the following formulas.

FCR = Feed conversion ratio = dry feed consumed (g)/gain in body wet weight (g).

PPV (%) = Productive protein value = [Protein gain in fish (g)/protein intake (g)] × 100.

ERV (%) = Energy retention value = [Energy gain in fish (kJ)/energy intake (kJ)] × 100.

Statistical analysis of weight gain and feed conversion ratio data was carried out using analysis of variance and Duncan's multiple range test (SAS, 1987) to identify the differences between means ($p < 0.05$).

3. Results

3.1. Gonadal development

The vast majority of 1-year fish under regime 1 (long day) remained sexually immature. An average of 5% (sample values = 0% and 10%) of fish sampled in March were spermiating males, and 5% (0% and 10%) reached the yolk granule stage (VO3) of oocyte development during May (Fig. 1). This was not the case for 2-year fish under the same regime as an average of 45% (30% and 60%) were spermiating males and 25% (20% and 30%) had reached the advanced vitellogenesis stage (VO4) of oocyte development by April (Fig. 2).

For both year classes, the fish on regime 2 (skeleton photoperiod) showed greater gonadal development compared to regime 1 (long day). A maximum of spermiating

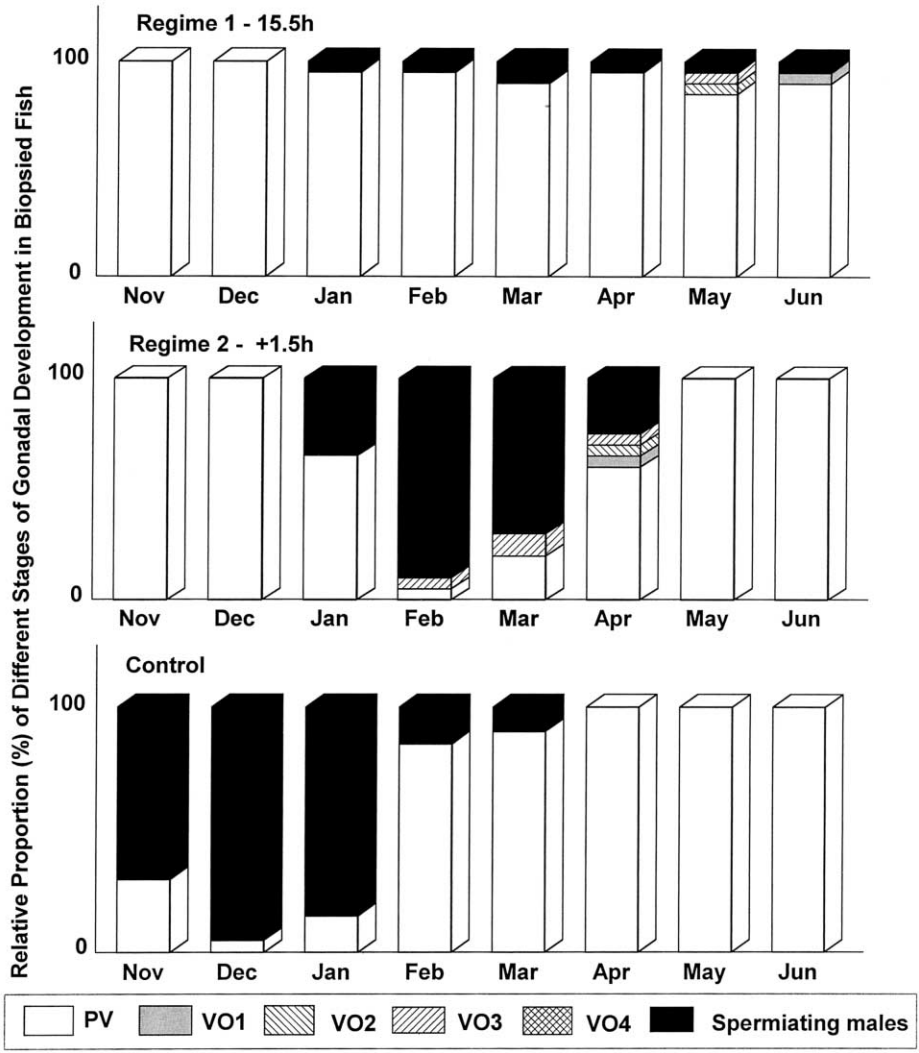

Fig. 1. Changes in gonadal development and maturation of 1-year gilthead seabream in biopsied samples ($n = 20$ fish) from the experimental photoperiod treatments. Bars indicate the relative composition of the different gonadal developmental stages in the sampled fish.

males occurred in February among year classes, 80% of the sampled 1-year and 50% of sampled 2-year fish. Ten percent of 1-year sampled fish reached the yolk granule stage (VO3) in March while 55% (50% and 60%) of 2-year sampled fish reached the advanced vitellogenesis stage (VO4) by March.

The control regime had the highest proportion of spermiating males in both year classes of sampled fish, reaching 95% (90% and 100%) in December for 1-year fish and 75% (70% and 80%) in March for 2-year fish. No oocyte development beyond PV stage

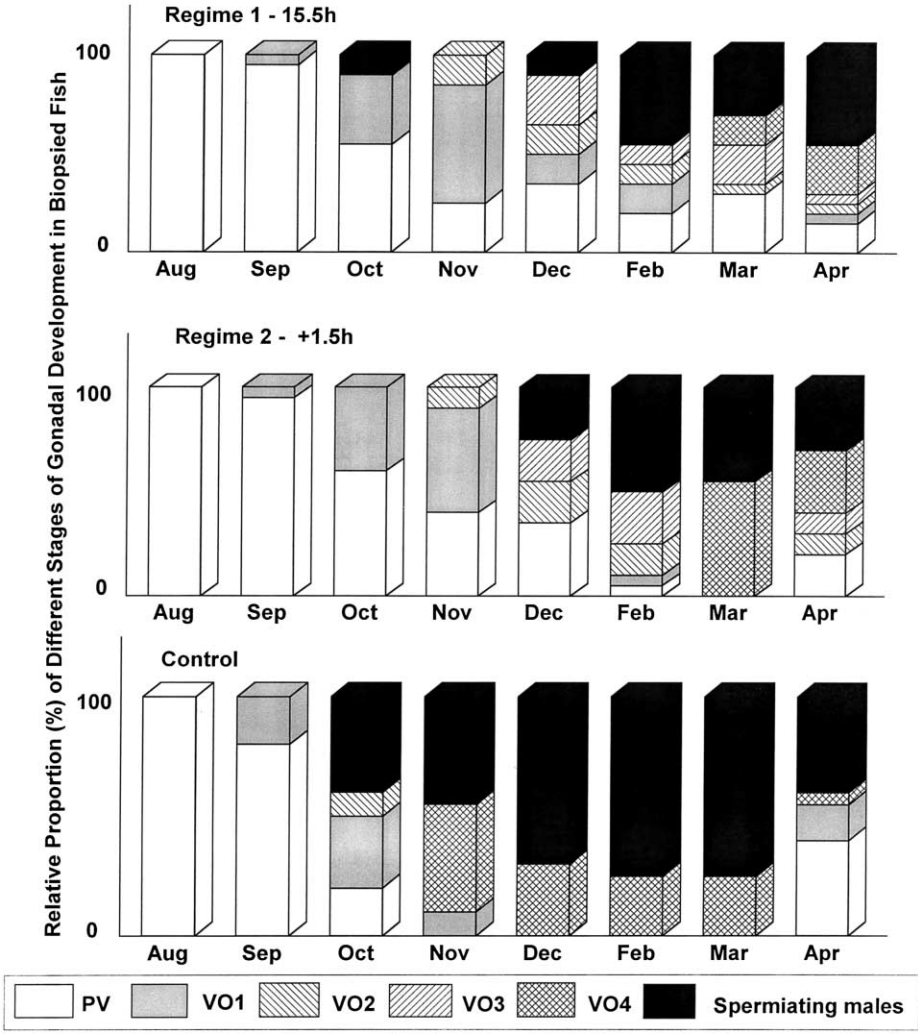

Fig. 2. Changes in gonadal development and maturation of 2-year gilthead seabream in biopsied samples ($n = 20$ fish) from the experimental photoperiod treatments. Bars indicate the relative composition of the different gonadal developmental stages in the sampled fish.

was observed in 1-year fish while a maximum of 45% (30% and 60%) of the 2-year reached the advanced vitellogenesis stage (VO4) in November.

3.2. GSI

The GSI value for 2-year fish at the start of the trial was 0.47. GSI values for regimes 1, 2 and control in March, 8 months into the trial, were 1.12, 4.73 and 2.14, respectively.

3.3. Spawning

The arrows in Figs. 3 and 4 indicate the approximate onset of sperm and egg release (spawning) as determined by a number of parameters. Actual spawning among 1-year fish may not have occurred due to the lack of sexually mature females in the population (Fig. 1). However, males could be stripped for milt (Fig. 1) and the populations underwent a reduction in growth rate (Fig. 3) in March (regime 2) and December (control), periods of the year parallel to the assumed onset of spawning in the older 2-year fish on these same regimes (Fig. 4). No reduction in growth occurred in 1-year fish on regime 1.

The onset of spawning was clearer among 2-year fish (Fig. 4) due to observed courting behavior, surface foam present in the fish tanks and a loss in average fish weight starting in March (regime 2) and December (control). Regime 1 fish did not undergo a weight loss nor were there other signs of spawning by the end of the trial.

In general, the onset of sperm and egg release in both year classes was delayed 2–3 months in regime 2 (skeleton photoperiod) fish and prevented in fish of regime 1 (long day).

3.4. Sex ratio

Analysis of the sex ratio data showed 1-year fish were mainly males or immature fish with a limited number of females in their early stages of development (cortical alveoli, lipid vesicle or yolk granule stages) (Fig. 1). However, 2-year fish were closer to having

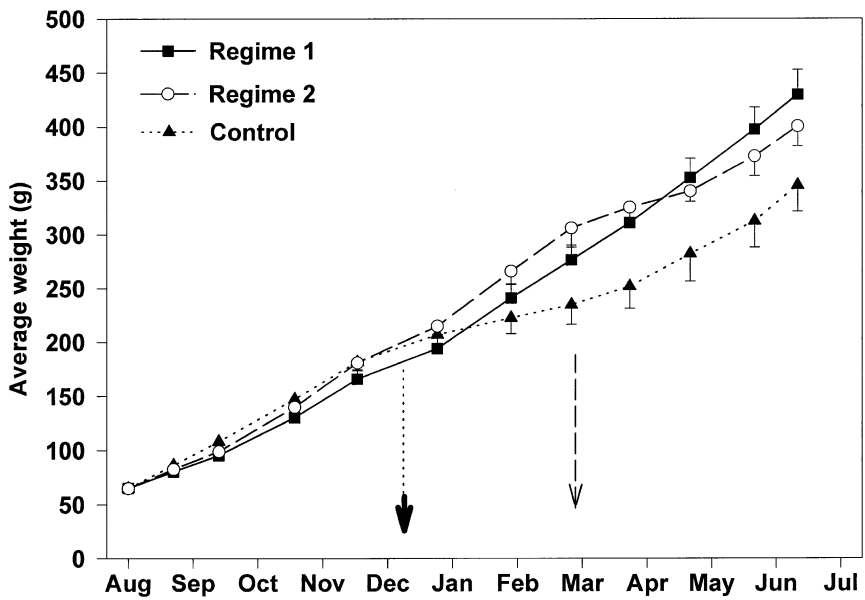

Fig. 3. Change in average weight (means ± SD, *n* see Table 2) of 1-year *S. aurata* maintained on three different photoperiod regimes. (↓) indicates onset of assumed sperm release in control photoperiod; (↓) indicates onset of assumed sperm release in regime 2 fish.

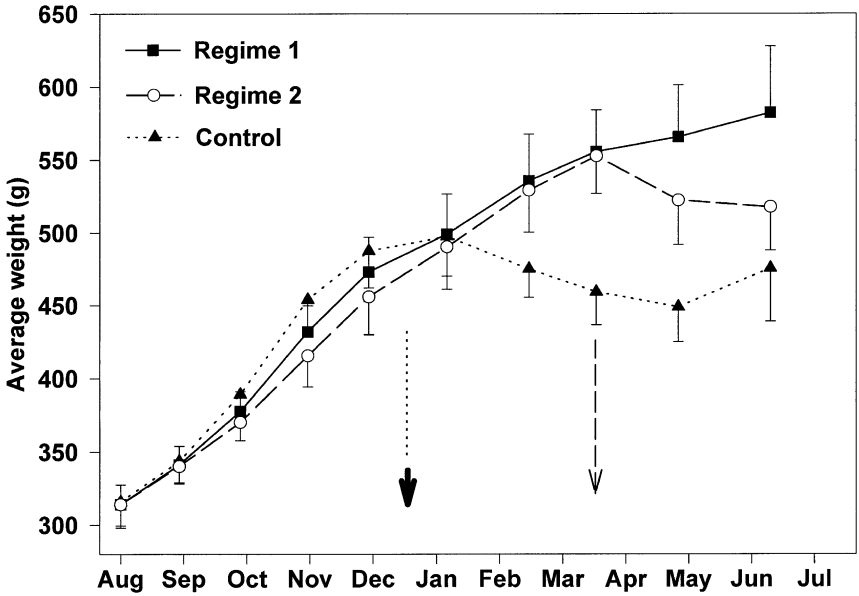

Fig. 4. Change in average weight (means ± SD, *n* see Table 2) of 2-year *S. aurata* maintained on three different photoperiod regimes. (⇓) indicates onset of assumed spawning of control photoperiod; (↓) indicates onset of assumed spawning of regime 2 fish.

equal numbers of both sexes around the time of anticipated spawning or trial termination in the case of regime 1 (Fig. 2).

3.5. Growth

Growth of 1- and 2-year fish under the different regimes appears in Figs. 3 and 4 and Table 2. Regime 1 (long day) fish of both ages grew best attaining 26% and 22% more weight than control treatments ($p < 0.05$) in 1- and 2-year fish, respectively. Fish under regime 2 (skeleton photoperiod) grew 17.4% and 8.8% better ($p < 0.05$) than controls, while poorest growth occurred in the control regime with 1-year fish undergoing a reduced growth rate and 2-year fish losing weight following the start of spawning.

3.6. Feed consumption

In general, daily feed consumption (Fig. 5) dropped with increased fish weight and the lower water temperatures of autumn and winter in all regimes of 1- and 2-year fish. In addition, feed consumption decreased to its lowest levels around the assumed onset of sperm and egg release and into the following month in the control and regime 2 treatments of both ages (Figs. 3–5). First year fish in regime 1 (Fig. 5A) did not undergo a similar reduction, although 2-year fish did display a small drop in feed intake during April (Fig. 5B).

Table 2
Average weight gain, feed consumption and protein and energy accumulation in gilthead seabream grown on the different photoperiod regimes

Photoperiod regime	Initial average weight (g) ± SD	Final average weight (g) ± SD [*]	Feed intake (g/fish)	PPV [**] (%)	ERV [**] (%)	FCR [*,**]
1-year fish						
1	64.9 ± 1.9 (n [***] = 12)	429.7[a] ± 22.9 (n [***] = 19)	785	–	–	2.15[a]
2	65.1 ± 2.6 (n = 12)	400.3[b] ± 18.2 (n = 24)	751	–	–	2.24[a]
Control	65.0 ± 1.5 (n = 12)	341.1[c] ± 34.2 (n = 21)	643	–	–	2.33[a]
2-year fish						
1	314.1 ± 13.4 (n = 11)	582.1[a] ± 45.5 (n = 19)	1086	12.6	15.3	4.04[a]
2	314.0 ± 14.5 (n = 11)	517.6[b] ± 29.8 (n = 18)	995	11.2	10.0	4.88[b]
Control	315.9 ± 17.7 (n = 11)	475.5[c] ± 36.6 (n = 18)	883	10.4	6.1	5.52[b]

(–) not determined.

[*] Values in the same column and year class of fish having the same superscript are not significantly different ($p > 0.05$) from each other.

[**] Average of duplicate tanks (n = 2).

[***] n = groups of 10 fish.

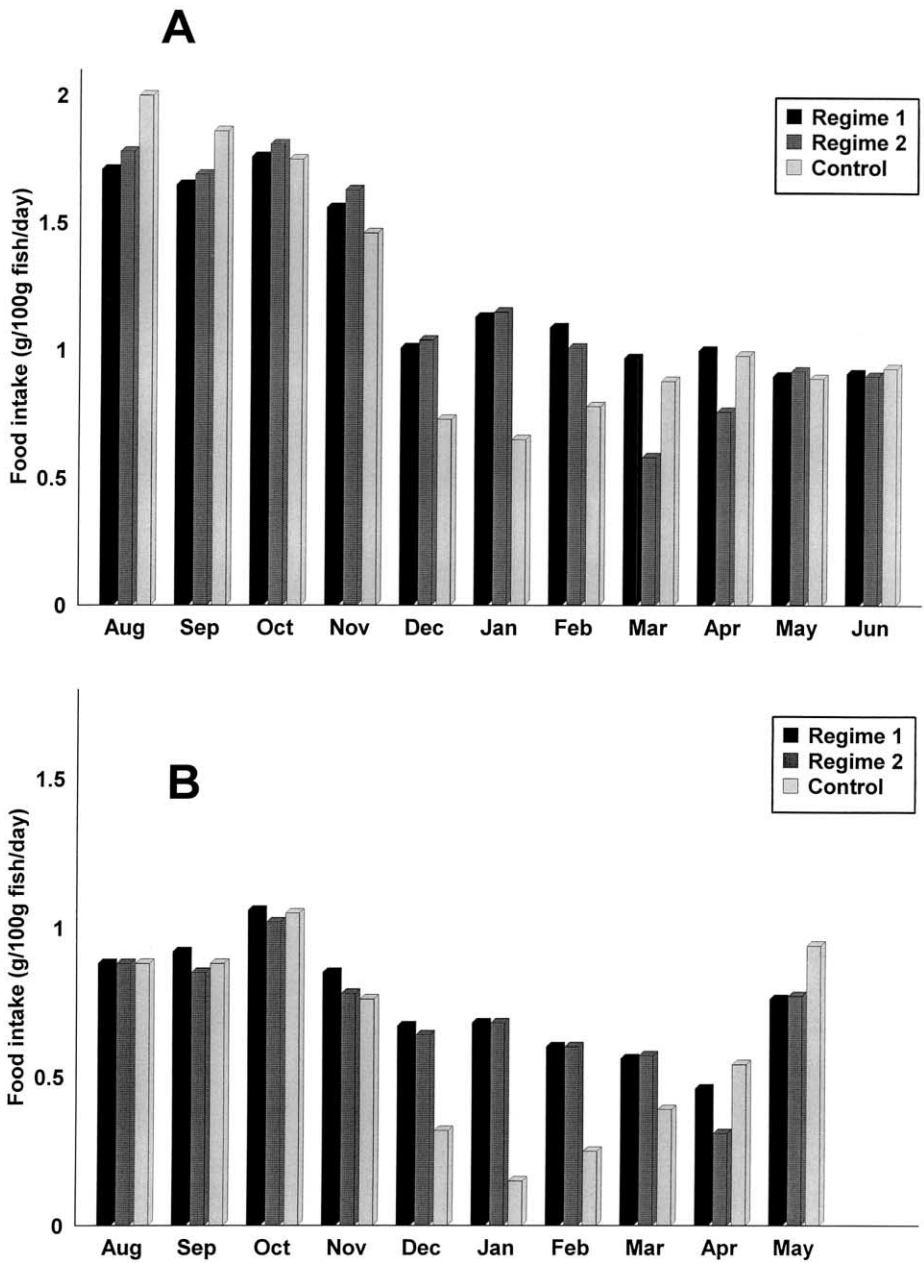

Fig. 5. (A and B) Feed consumption of 1- (A) and 2- (B) year gilthead seabream during the experimental trials. Columns represent monthly average treatment values for all experimental regimes, calculated from daily feed consumption data and given as daily food intake (g)/100 g of fish.

Table 3
Composition of the 2-year fish (g/kg wet weight) during the feeding trial

	Protein	Lipid	Ash	Energy (MJ/kg)
Initial	162	185	37	11.11
Regime 1	181	178	42	10.61
Regime 2	184	152	40	9.76
Control	184	130	43	8.98

Feed conversion ratio (FCR) followed the same general trend as growth although not always with the same statistical significance. The treatment with the best growth (regime 1-long day) had lower FCR while the control with the poorest growth had high FCR. Regime 2 (skeleton photoperiod) with intermediate weight gain had intermediate FCR values (Table 2).

The results of feed consumption, body composition analysis and the subsequent calculation of protein and energy utilization for the treatments with 2-year fish are given in Tables 2 and 3. Both protein and energy accumulation, which are expressed as productive protein value (PPV) and energy retention value (ERV), followed a similar pattern with growth and FCR. The longest day photoperiod regime (1) had the most efficient buildup of body protein with accumulation decreasing in subsequent treatments, the control being the lowest. ERV values had a wider range but followed the same pattern with regime 1 having 2.5 times greater energy retention than the control. Differences in body composition were most apparent in the lipid content with regime 1 having the highest and the control the lowest.

4. Discussion and conclusions

Maintenance of seabream on a constant photoperiod equivalent to the longest day of the year, 15.5L:8.5D (regime 1) from July onwards, clearly postponed gonadal development and as a result prevented the females from spawning. This is true for both 1-year fish, which were mainly males, and 2-year fish having approximately equal numbers of both sexes. The addition of the 1.5-h pulse of fluorescent light beyond the normal daylight period (regime 2) was given in these experiments in such a way as to try and imitate the longest day constant photoperiod even though the fish did not have light for the whole 15.5 h. This “skeleton photoperiod” was not as effective as the constant light regime in postponing gonadal development or preventing spawning. Therefore, the assumption that this dark period would be ignored and not translated into a signal for shortening of the day, was incorrect. The “skeleton photoperiod” did however, postpone both processes by up to 3 months resulting in weight gain over the control group and the extension of the optimal time for marketing these fish into the early spring.

In our experiment, a likely explanation for the effect of the 1.5-h pulse involves the fact that fish under the “skeleton photoperiod” regime were exposed to natural daylight followed by a period of darkness of up to 225 min, and then a 1.5-h pulse of fluorescent

light which started 14 h after sunrise. Even though the period from sunrise to the end of the 1.5-h pulse was kept a constant 15.5 h throughout the experiment, these fish did experience a shortening of natural daylight and a resulting increased dark period up until December 21, thus shortening the possible overlap between light and the putative "photosuppressive" phase. It is known that this shortening of daylight is the stimulus for sexual maturation in seabream (Zohar et al., 1995). The additional light pulse these fish received probably mitigated the effects of the natural day shortening but could not override it completely and as a result, gonadal development and spawning were only postponed by 3 months.

Karlsen et al. (1999) noted differences in the effect of continuous light with Atlantic cod depending upon the nature of the light. They differentiated between continuous light that was superimposed on natural light in sea cages as reported by Hansen et al. (1995) and continuous light from a single source in indoor tanks. In both cases, continuous light enhanced growth but only in the indoor tanks was maturation arrested, while it was delayed 4–6 months in the sea cages. They suggested that difference in light intensity between night and day may be critical in aiding fish to perceive photoperiod as continuous or changing. This may also apply in the case with seabream as fish in the "skeleton photoperiod" experienced greater daily fluctuations in light intensity during their long day as compared with the fish on a continuous 15.5 h of light.

The postponement of gonadal development resulted in the continued growth of fish as seen in the significantly higher average weights of regime 1 (long day) and 2 (skeleton photoperiod) fish. Energy sources from the feed that would normally be used in the development of eggs and sperm are shunted into somatic growth with the resulting added weight gain. This is similar to what Kadmon et al. (1985a) showed in seabream maintained on a constant long day. Their fish continued growing during the spawning season while growth of control fish on a natural photoperiod was completely arrested. The authors attributed the arrested growth to the onset of gonadal recrudescence, its associated mobilization of nutrients in the fish and reduced feed consumption.

The GSI values of 2-year fish in March were consistent with the reproductive activity of the different groups at the time. Control fish were at least 3 months from the start of spawning and their intermediate GSI might represent the process of gamete depletion. Regime 1 (long day) fish were still delayed in their development and spawning, hence the low GSI. Regime 2 (skeleton photoperiod) fish were in the process of spawning so the high GSI of 4.73 would be anticipated. A comparison with more recent data from NCM (Meiri—unpublished data) for natural photoperiod seabream populations (the equivalent of the control regime) indicates March GSI values could be higher (7.0–9.0). Moreover, comparisons between these two populations is complicated by the range of factors which influence GSI. Differences between the nutritional status of the fish, their concentration in the holding tanks, seawater temperature and the average weight of the fish can all influence their relative GSI values.

The feed conversion ratio followed the same general pattern as weight gain in these trials. Although the FCR values were not always statistically different from each other, in general, there was a trend toward a poorer conversion of feed to biomass with a complete lack of photoperiod postponement of maturation and spawning. Control fish of both sexes were less efficient in using food, probably as a result of releasing their

developed sex products into the water after having used nutrients from food for their development. The seabream's ability to rapidly incorporate feed nutrients into developing eggs and the volume of eggs produced by an individual help support this assumption, at least for female fish. The observed differences in FCR values between regime 1 and control fish (8.4% lower in 1-year and 36.6% lower in 2-year fish) are a direct measure of this nutrient loss to reproduction. The poorer conversion seen in all treatments of 2-year fish when compared with 1-year fish is partially a result of the significant differences in composition of the feeds used to culture the fish and, to a lesser extent, a result of poorer feed conversion usually seen in larger fish (Brett and Groves, 1979; Henken et al., 1986; Lupatsch and Kissil, 1998).

The reduction in feed intake that we observed coinciding with the assumed onset of sperm and egg release is similar to the findings of Kadmon et al. (1985a). They eliminated water temperature as a possible cause of the reduction and associated it with sexual differentiation and gonadal recrudescence. Fish in the present study were fed twice daily to satiation with no attempt made to restrict feeding. It is assumed, therefore, that the observed feed reduction is also related to the reproduction process.

The manipulation of photoperiod as previously mentioned is being used to increase the availability of stockable fish in a number of ways: increased growth and survival of young fish, extended spawning periods, and out of season spawning. In addition it can be used to increase growth and feed efficiency in juvenile seabream (Silva-Garcia, 1996), suggesting a commercial role for photoperiod in seabream culture. To our knowledge though, the use of photoperiod to postpone gonadal development and spawning to conserve body reserves is not being applied commercially on a wide scale.

Year round production of gilthead seabream juveniles is routinely practiced in some of the Mediterranean countries where cultivation is underway. With the increased demand for larger market size fish seen in recent years, fish may spend more time in culture systems. Although use of more efficient feeds, better growing conditions and use of selected faster growing strains has helped reduce culture time shortening the time to market size, farmers will still have to overwinter fish to meet market demand for larger size. The farmers' ability to postpone gonadal development and spawning of his fish will mean more efficient overwintering techniques resulting in continued weight gain with significant savings in feed.

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