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Effects of temperature on growth and metabolism in a Mediterranean population of European sea bass, Dicentrarchus labrax

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Abstract: Growth and metabolism of juvenile European sea bass of a Western Mediterranean population were assessed at six constant temperatures (13, 16, 19, 22, 25 or 29 °C) in an 84-day trial. Duplicated groups of 84 fish (initial weight 80±1 g) were held under O2-concentrations close to saturation (8–7 mg l−1) and were fed to satiation. Mass gain increased as temperature increased from 13 to 25 °C. At 25 and 29 °C, growth was similar up to day 72, but a 6% decrease was observed by day 84 at 29 °C. Days 0–84 specific growth rates (SGR) were 0.45%, 1.29% and 1.21% day−1 at 13, 25 and 29 °C, respectively. The estimated temperature (T) for maximum SGR was 26 °C (SGR=1.715−0.322T+0.022T2−4.233e−4T3). Feed intake (FI) increased with temperature being 1.45–1.46% day−1 at 25–29 °C and the estimated temperature for maximum FI was 27.5 °C (FI=1.453−0.214T+0.016T2−2.916e−4T3). Feed efficiency (FE) averaged 1.01–1.04 at 19–25 °C, was lower at 16 and 13 °C (0.9) and maximum FE was estimated to occur at 24 °C (FE=1.318−0.103T+7.174T2−1.395T3). The main difference in fish body composition related to temperature was a higher crude fat concentration at 13–16 °C at the end of the experiment (day 84). Protein retention was 38% (g g−1) at 25 °C (NS differences in 22–28 °C range). Ammonia excretion (TAN, mg N kg−1 day−1) was positively correlated to temperature as it was dependent on feeding rate (FR, g kg−1 day−1) (TAN=−496.5 FR+24.4 FR2+2685). O2-consumption (MO2R, mg kg−1 h−1) was influenced by temperature (MO2R=10.83T+4.48) and by FR (MO2R=−206.8FR+10.6FR2+1142).

Keywords: Feeding, Metabolic rate, Thermal requirement, Fish culture, Oxygen consumption

1. Introduction

Several biotic and abiotic factors influence the growth of fish (Brett and Groves, 1979; Jobling, 1996) and water quality requirements of marine fish species farmed in Europe (turbot, *Scophthalmus maximus*; European sea bass, *Dicentrarchus labrax*; cod, *Gadus morhua*) have been examined for development of land-based rearing systems (Blancheton, 2000; Björnsson et al., 2001; Pichavant et al., 2001; Person-Le Ruyet, 2002). In turbot, temperature and oxygen and their interactions exhibited long-term effects on growth but there are differences between fish from different geographic areas (Bœuf et al., 1999; Imsland and Jonassen, 2001; Imsland et al., 2001;).

Water quality requirements are less well known for sea bass than turbot, even though sea bass is an important species in European marine culture (50000 tonnes produced in 2002, compared to 5000 for turbot). Juvenile sea bass seem to cease growing at 11-15°C and to grow fast at 22-25°C and lethal limits may be 2-3°C and 30-32°C (Barnabé, 1991). Russell et al. (1996) reported that growth of juvenile sea bass in British waters (at the northern limit of the species range) did not occur at 7°C and was high at 18°C. However thermal effects interact with both external (oxygen, salinity, food supply) and intrinsic biological factors (age, population, strain). For example when feeding or oxygen availability is restricted, the temperature at which fish growth best is lower than when feeding and oxygen supply are not limiting (Jobling, 1996). There may also be intra-specific differences in growth-temperature relations for populations from different geographic regions (Conover et al., 1997; Imsland and Jonassen, 2001). In juvenile sea bass, the effects of temperature on growth have not been well established under controlled environmental conditions with reference to fish origin and feeding conditions.

The aim of this study was to assess the effects of temperature on growth of sea bass from a Mediterranean population. To this end, feeding, growth and metabolic responses were examined in juveniles exposed to constant temperatures that covered the range typical of Mediterranean coastal waters during winter and summer (13-29°C).

2. **Material and methods**

2.1. Fish and rearing conditions

The experiment was carried out using 20 month old hatchery reared juveniles previously held for 4 months in 4-m^2 tanks supplied with running seawater (34-34.5‰ salinity; 22-23°C, oxygen 90-95% saturation). The photoperiod was maintained at 18 L: 6 D and maximum light intensity was 50 lux at the water surface. The fish were fed a commercial extruded dry pellet (Le Gouessant®, protein 44.1% and crude fat 22.5%) distributed 8 h per day using belt feeders. For the experiment, 1008 fish (previously individually weighed and sorted) were randomly distributed among the 12 tanks (1-m^2 tanks with an effective volume of 450 l). The fish were allowed to adapt to the new conditions for 13 days. They were held in water at 22°C with an O_2-concentration of 7.8 mg l^{-1} [105% saturation prior to fish feeding, using an oxygen supplementation device (Person-Le Ruyet et al., 2002)]. Water exchange rate was 160% h^{-1}. The fish were hand-fed to apparent satiation twice a day at 0900 and 1400.

2.2. Experimental design

The 84-day experiment was carried out using duplicate groups of 84 fish each, held at 13, 16, 19, 22, 25 or 29°C. On day 0, the initial mass per tank was assessed by weighing all fish in the tank. The fish were fasted for 24 h and anaesthetised in a solution of ethylene-glycol-monophenyl-ether (0.5‰) before weighing. Mean fish weight was ca. 82 g and stocking density was ca. 16 kg m^{-3} (Table 1). From day 0 onwards, two tanks were maintained at 22°C, whereas in other treatments the temperature was gradually increased or decreased by 3°C day^{-1} until the test temperature was attained (within 2-3 days). From then on, temperature was maintained constant until the end of the experiment. O_2-concentration was checked in the tank outlet water once a day prior to feeding and was adjusted as required by changing O_2 injection to maintain 100-105% saturation. Total gas pressure was checked with a tensionometer (300 C Novatech®) at the start and the end of the experiment. Salinity (WTV®) and pH (Orion 901 fitted with a Fermprobe®electrode) were measured weekly and total ammonia nitrogen (TAN) was measured once a month (automatic colorimetric method as described in Dosdat et al. (1996). Fish were hand-fed twice a day to apparent satiation; any uneaten food was collected in a waste trap fitted to the outflow, and feed intake was calculated for each meal as feed provided minus feed waste.

Six fish were randomly removed from each tank on days 7, 14, 28, 56 and 84 for blood and tissue analysis and they were weighed for mass estimation. As a result stocking density was maintained below 30 kg m^{-3} and water quality was consistent (Table1).

2.3. Studied parameters

Growth was estimated by weighing all fish on days 0, 14, 28, 42, 56, 70 and 84. Specific growth rate (SGR, % day^{-1}) was calculated as: $100 \times (\ln w_f - \ln w_i) day^{-1}$, where w_i and w_f are the initial and final mean body weights, respectively. The coefficient of variation for body weight (CV, %) was calculated as: 100 x standard deviation x mean body $weight^{-1}$.

Some fish were removed from the tanks at intervals so daily feed intake (FI) and apparent feed conversion efficiency ratio (FE) were estimated by taking into account the average mass per t_1–t_2 period, (day1-7, 8-14, 15-28, 29-56, 57-84) using the following expressions:

- FI: 100 x (mean daily mass of dry feed ingested, g x mean wet fish $mass^{-1}$, g) where mean fish mass = (fish mass at t_2 + fish mass at t_1) 2^{-1} and fish mass = mean body weight x fish number;
- FE: fish mass gain, g x dry feed $ingested^{-1}$, g.

Body composition of whole fish was determined on 3 samples of 4 fish each taken from 3 tanks on day 0 and on samples taken from each tank on day 84. Fish were minced and moisture was determined on homogenates (24 h at 105°C) that were subsequently freeze-dried and ground before further analyses. Chemical analyses of fish and feed were performed in triplicate for each sample according to AOAC (Association of Official Analytical Chemists, 1984) methods: ash (7 h at 550°C), crude fat (dichloromethane extraction with a Sostec System Ht®), and crude protein (Dumas method with an Elementary NA 2000®, $N \times 6.25$). Protein retention was calculated as: 100 × (fish protein gain, g x feed protein $intake^{-1}$, g),

where protein intake = feed ingested x feed protein concentration and, protein gain = (final mean fish mass x final fish protein concentration) - (initial mean fish mass x initial fish protein concentration).

Excretion of total ammonia nitrogen (TAN) and urea-N were estimated on days 49-55 from measurements of TAN and urea-N concentrations in the inlet and outlet water made using automatic colorimetric methods (Dosdat et al., 1996). Measurements were undertaken over 3 consecutive days by sequential sampling over 24 h using a peristaltic pump. TAN and urea-N excretion rates (mg kg^{-1} day^{-1}) were calculated as: (outlet concentration - inlet concentration) × Q_w W^{-1}, where Q_w = flow rate (l day^{-1}) and wet fish mass (W) was estimated by inference from the growth curve.

Oxygen consumption of fed fish (MO_2R, µmol O_2 g^{-1} h^{-1}) was estimated at the same time as nitrogen excretion from the difference in O_2-concentration in the inlet and outlet waters of each tank after correction for O_2 variations measured in a tank without fish. O_2-concentrations were monitored in each tank twice per hour during one minute using procedures described by Burel et al. (1996).

2.4. Data analysis

All results are expressed as mean ± SE. Statistical analyses were conducted using Statistica for Windows. Changes in fish mass in relation to temperature and time were tested using two-way nested ANOVA, with tanks as the nested factor. One-way ANOVA was used to test for differences for SGR, FI, FE, body composition, TAN excretion rates and MO_2. Significant ANOVAs were followed by a *post hoc* multiple comparison test (Newman-Keuls

test). Differences were considered significant at $P < 0.05$. Prior to ANOVA analysis, data expressed in %, were arcsinus square-root transformed.

Different mathematical functions were applied to test the thermal responses of the studied parameters using Sigmaplot. For each parameter, the best curve fitting (to linear, exponential or polynomial models) was selected and for SGR, FI and FE, the maximum thermal response was directly calculated from the selected equation.

3. **Results**

Temperature remained stable over the 84-day experiment (CV for temperature was 9% at 13°C and 4% at 29°C). Water quality was stable in all groups although there were some differences in ammonia concentration and pH between temperature groups, and O_2-concentrations were close to saturation, averaging 8.3 mg l^{-1} at 13°C and 7.1 mg l^{-1} at 29°C (Table 1).

Table 1. Temperatures tested in the 84-day experiment and data related to juvenile sea bass and to water quality.

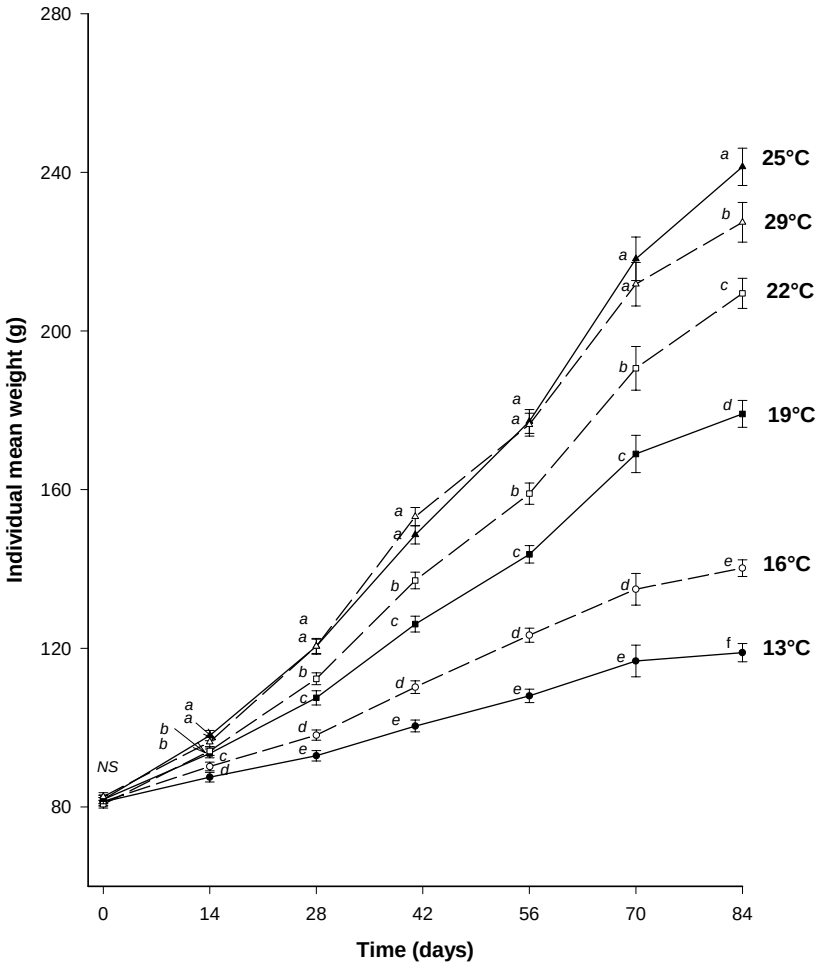
Temperature (°C)	13.4 ± 0.1	16.2 ± 0.1	18.9 ± 0.1	21.9 ± 0.1	24.9 ± 0.1	28.8 ± 0.1
Day 0 fish number	84	84	84	84	84	84
Day 0 fish weight (g)	81.3 ± 1.1	81.4 ± 1.0	81.9 ± 1.0	80.7 ± 1.0	81.9 ± 1.1	82.6 ± 1.0
Day 0 weight CV (%)	11.6	10.6	11.2	10.4	11.8	10.9
Day 0 stocking density (kg m^{-3})	16.3	16.3	16.4	16.1	16.4	16.5
Day 84 fish number	52	52	52	52	52	52
Day 84 fish weight (g)	118.9 ± 2.3	140.2± 2.1	179.1 ± 3.4	209.5 ± 3.8	241.4 ± 4.7	227.4 ± 5.0
Day 84 weight CV (%)	13.9	11.2	14.1	13.4	14.1	15.9
Day 84 stocking density (kg m^{-3})	14.7	17.4	22.2	25.9	29.9	28.1
O_2-conc. (mg l^{-1})	8.3 ± 0.7	8.5 ± 0.7	8.4 ± 0.7	7.8 ± 0.6	7.4 ± 0.7	7.1 ± 0.5
O_2-conc. (% saturation)	96	104	109	106	107	109
pH	8.20 ± 0.02	8.15 ± 0.07	8.10 ± 0.02	8.02 ± 0.03	7.97 ± 0.03	7.96 ± 0.03
Salinity (‰)	34.8 ± 0.1	34.8 ± 0.1	34.9 ± 0.1	34.9 ± 0.1	35.0 ± 0.1	35.0 ± 0.1
TAN (mg l^{-1})	0.07 ± 0.02	0.13 ± 0.02	0.13 ± 0.02	0.26 ± 0.02	0.32 ± 0.04	0.27 ± 0.04

Means are given with SE; day 0 fish weight, n=168; day 84 fish weight, n=104; weight CV, n=2; O_2-concentrations, n=84; pH and salinity, n=12; Total Ammonia Nitrogen (TAN), n=3.

In all groups, the fish appeared healthy and no mortality was observed. Mass gain increased as temperature increased from 13 to 25°C with significant differences between temperature groups from day 28 onwards (Fig. 1). At 25 and 29°C growth was similar up to day 72, but a significant decrease was observed on day 84 at 29°C (mean weight 6% lower at 29 than at 25°C). On day 84 fish weight dispersion was low in all groups (Table 1). Significant differences in CV for weight related to temperature were observed ($P = 0.003$), CV being higher at 29°C (16%) and lower at 16°C (11%) than in the other groups.

Fig.1- Changes of mean weight over time in relation to the 6 constant temperatures tested. Means are given with standard error (n = 2 replicates). Letters indicate statistical differences between temperature groups, means not sharing a common letter are significantly different (P<0.05) and NS = no significant differences (P> 0.05).

Fig.1

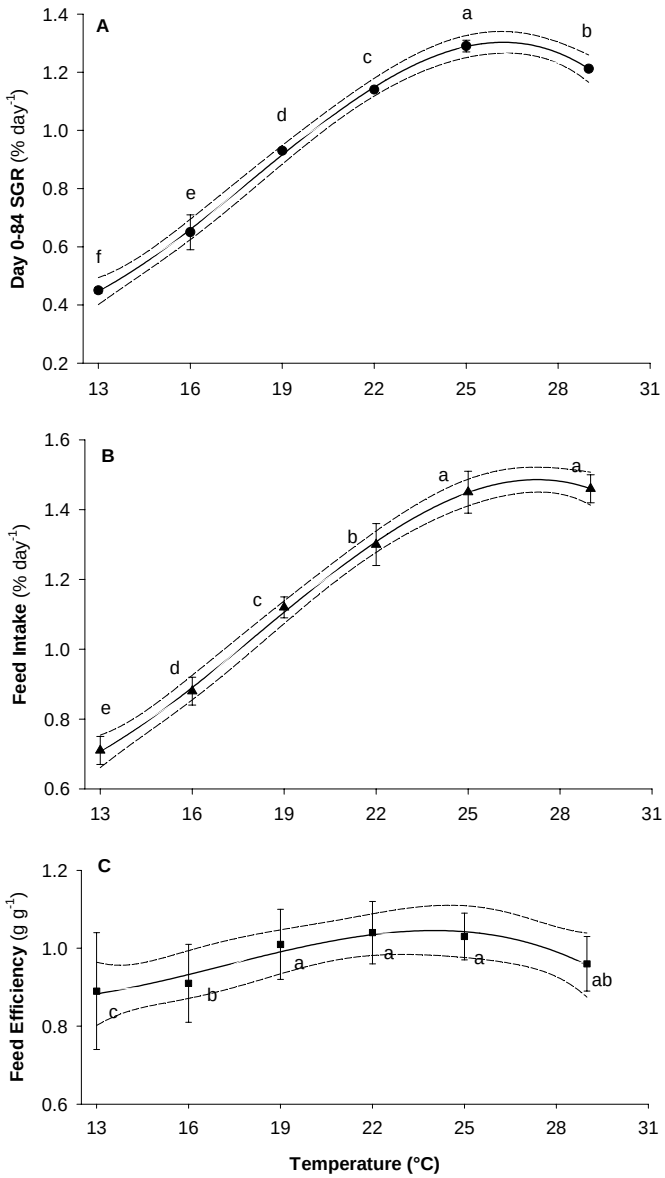


Day 0-84 specific growth rate (SGR) increased with temperature up to a maximum at 25°C followed by a slight but significant decrease at 29°C (Fig. 2A). Feed intake (FI) increased with temperature up to a maximum at 25-29°C (NS differences between 25 and 29°C), (Fig. 2B). Feed efficiency ratio (FE) was maximum at 19-25°C, a significant decrease was

observed at 16 and 13 °C and a NS decrease at 29°C. The relationships between SGR, FI, FE and temperature (T) could be described by the following equations:

Fig.2- Day 0-84 Specific Growth rate (A), Feed Intake (B) and Feed Efficiency ratio (C) in relation to temperature.
Means are given with standard error (n = 2 replicates) and dashed lines represent confidence intervals. Letters indicate statistical differences between temperature groups, means not sharing a common letter are significantly different (P<0.05).

Fig.2



$SGR = 1.715 – 0.322\ T + 0.022\ T^2 – 4.233e^{-4}\ T^3$ ($n = 12$, $r^2 = 0.999$).

$FI = 1.453 – 0.\ 214\ T + 0.016\ T^2 – 2.916e^{-4}\ T^3$ ($n = 12$, $r^2 = 0.999$).

$FE = 1.318 – 0.103\ T + 7.174\ T^2 – 1.395\ T^3$ ($n = 12$, $r^2 = 0.944$).

Calculated temperatures for maximum SGR, FI and FE were 26.1°C, 27.5°C and 23.9°C respectively.

Some differences in fish body composition related to temperature were observed (Table 2). On day 84, body fat concentration was highest at 13-16°C, and protein retention was highest at 25°C but without significant differences in the 22-29°C range. There was also some changes with time in fish composition as in the 22°C group (control temperature group) a significant increase in body crude fat concentration and a decrease in percentage of water was observed over the 84-day experiment.

Table 2. Percentage compositions of the test feed and juvenile sea bass at the start (day 0) and end of 84 days of rearing under different temperature conditions.

Age (days)	T° (°C)	Water (%)	Protein (%)	Fat (%)	Ash (%)	Protein retention (g g^{-1})
Day 0	22	66.9 ± 0.4	17.9 ± 0.2	11.4 ± 0.1	4.0 ± 0.1	
Day 84	13	61.8 ± 0.2 a	17.4 ± 0.4 ab	18.0 ± 0.5 a	3.6 ± 0.1 ab	25.2 ± 0.1 d
	16	61.2 ± 0.1 b	17.1 ± 0.1 b	18.4 ± 0.1 a	3.2 ± 0.2 b	29.7 ± 2.1 c
	19	61.8 ± 0.1 a	17.6 ± 0.1 ab	17.3 ± 0.3 b	3.7 ± 0.1 ab	35.1 ± 0.1 b
	22	61.8 ± 0.1 a	17.7 ± 0.3 a	16.8 ± 0.3 b	3.6 ± 0.2 ab	37.2 ± 0.3 ab
	25	60.7 ± 0.2 c	17.7 ± 0.2 a	17.9 ± 0.1 a	3.3 ± 0.1 b	38.3 ± 0.4 a
	29	61.7 ± 0.1 a	17.8 ± 0.1 a	16.9 ± 0.4 b	4.0 ± 0.4 a	35.8 ± 0.2 ab
Diet		8.4 ± 0.1	44.1 ± 0.2	22.5 ± 0.3	9.6 ± 0.1	

Means are given with SE (n=2 replicates). Letters indicate statistical differences between temperature groups, means not sharing a common letter are significantly different (P <0.05).

The daily TAN excretion per fish mass was positively correlated to temperature (Fig. 3A) as it was dependent on feeding rate, FR (Fig. 3C). Daily TAN excretion rate was 2.7 times higher at 25°C than at 13°C and there were no significant differences in the 22-29°C

range (Table 3). The relationship between TAN excretion (mg N kg^{-1} day^{-1}) and FR (g kg^{-1} day^{-1}) was described as: TAN = - 496.5 FR + 24.4 FR^2 + 2685 (n = 12, r^2 = 0.96). Daily urea-N excretion rate was not significantly affected by temperature, so the ratio of urea-N to TAN + urea-N excreted was affected by temperature, averaging 22 at 13-19°C and 13 at 22-29°C (Table 3).

Fig. 3- Changes in mean total ammonia nitrogen (TAN) excretion and O_2-consumption in relation to temperature (A, B) and feeding level (C, D).
TAN excretion and O_2-consumption of feeding fish were measured on days 49-55. Means are given with standard error (n = 2 replicates). Letters indicate statistical differences between temperature groups, means not sharing a common letter are significantly different (P<0.05).

Fig.3

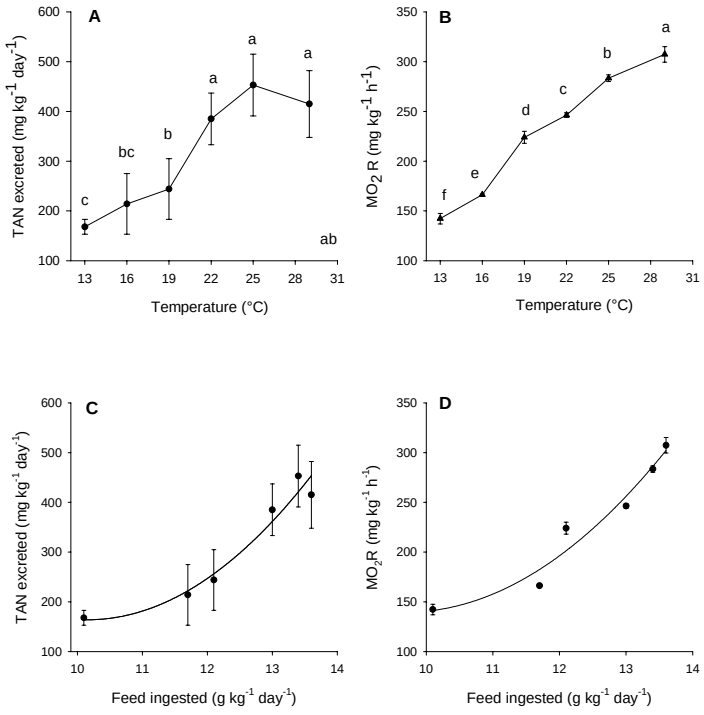


Table 3. Nitrogen excretion data in juvenile sea bass fed to apparent satiety and reared under different temperature conditions for 49 days.

Temperature (°C)	13	16	19	22	25	29
Fish weight (g)	108 ± 2	123 ± 2	144 ± 2	159 ± 2	177 ± 3	176 ± 3
TAN (mg N kg^{-1} day^{-1})	168 ± 15 c	214 ± 61 bc	244 ± 61 b	385 ± 52 a	453 ±62 a	415 ± 67 a
Urea-N (mg N kg^{-1} day^{-1})	50 ± 5 a	61 ± 5 a	61 ± 2 a	62 ± 2 a	62 ± 4 a	67 ± 47 a
Urea-N x 100 $(Urea\text{-}N+TAN)^{-1}$	23	22	20	14	12	14
TAN N $ingested^{-1}$ (%)	23 ± 2	26 ± 4	28 ± 2	38 ± 3	45 ± 5	41 ± 5

Means are given with SE (n=2 replicates). Letters indicate statistical differences between temperature groups, means not sharing a common letter are significantly different (P <0.05).

The oxygen consumption (MO_2R, mg kg^{-1} h^{-1}) was positively correlated to temperature (T) and could be described as: $MO_2R = 10.83\ T + 4.48$ (n = 12, $r^2 = 0.97$), (Fig. 3B). The relationship between MO_2R and FR (g kg^{-1}) could be expressed as: $MO_2R = -206.8\ FR + 10.6\ FR^2 + 1142$ (n = 12, $r^2 = 0.96$), (Fig. 3D).

4. **Discussion**

Temperature plays an important role in governing growth of sea bass via its effects on feeding and metabolism. Fish were fed to apparent satiety and O_2-concentrations were maintained over 7 mg l^{-1} as maybe reduced below 6 mg l^{-1} (Pichavant et al., 2001). TAN concentrations were low compared to concentrations that lead to reduced growth in sea bass, *i.e.* 5-10 mg l^{-1} TAN (Person-Le Ruyet, 2002; Lemarié et al., 2003).

The growth of the juvenile sea bass from this Mediterranean population (identified as a Western Mediterranean strain, Ky, personal communication) was estimated to be maximum at 26°C with growth peaking within a narrow range of temperatures. In cooler water, growth was markedly depressed (SGR was 65% lower at 13°C than at 26°C) and the drop in growth

rate resulted primarily from a decrease in feed intake. At the other extreme tested, 29°C, growth was only slightly depressed compared to growth at 26°C. The temperature range over which feed conversion efficiency (FE) was close to maximum was broader than the temperature range for maximum growth, 19-25°C, and, the range was displaced towards lower temperatures. The highest N retention was observed in the 19-25°C range, whereas weight gain at 13-16°C involved the greatest increase in fat body concentration. Growth rates obtained at 22°C and recorded feed conversion efficiency were in the upper range of values reported for juvenile sea bass (Boujard et al., 1996; Azzaydi et al., 1999; Gardeur et al., 2001; Pichavant et al., 2001). Whole body composition and N retention were also in agreement with data obtained under similar feeding and thermal regimes (Hidalgo et al., 1987; Ballestrazzi et al., 1998; Dias et al., 2001).

The thermal responses of European sea bass in terms of feeding and growth performances are in line with other studies on teleosts (Woiwode and Adelman, 1991; Jobling, 1994, 1996). For example, in hybrid bass (*Morone saxatilis* x *M. chrysops*) temperature for maximum growth was 26.8°C, FI increased with temperature up to 29.2°C and feed conversion efficiency peaked at 21.2°C (Woiwode and Adelman, 1991). Our study revealed the capacity of a Mediterranean population of sea bass to adapt to 29°C and to grow as fast as at 25°C for 2 months when O_2-concentration and feed supply were not restricting. For longer exposure, the decline in growth rate following longer exposure to 29°C concomitant with a slight decrease in feed efficiency is a novel finding. The results suggest that the upper temperature for juvenile growth over prolonged periods may be close to 29°C, but the temperature responses we observed appeared slightly elevated in comparison with farm experience (Barnabé, 1991). The higher temperature for maximum growth observed in our study may be related to the genetic or geographic origin of fish considering that

differences in muscle growth between Atlantic and Mediterranean populations have been reported for larval sea bass (Ayala et al., 2001).

Sea bass O_2-consumption and ammonia excretion were dependent on temperature and on feed intake, as is generally found in fishes (Wood, 1993; Jobling, 1996). O_2-consumption measured under routine conditions (MO_2R) increased linearly with increasing temperature, being about twice as high at 25°C as at 15°C. This is in general agreement with results obtained by Claireaux and Lagardère (1999) for larger sea bass (620 g). The 8% increase in MO_2R between 29°C and 25°C concomitant to a decrease in growth may have resulted from elevated maintenance costs at 29°C, as described by Jobling (1996). Mean daily ammonia excretion rate was about 3 times higher at 25°C than at 13°C, and there was an exponential relationship between nitrogen excretion, feeding and temperature. In salmonids, nitrogen excretion rate has been modelled in relation to temperature and nitrogen intake using both exponential and linear expressions (Lyytikäinen and Jobling,1999). The results in our study gave a better fit to an exponential than a linear model. Ammonia excreted represented 23-26% of N ingested at 13-19°C compared to 45-41% at 22-29°C; the highest values at the highest temperature probably resulted from differences in nitrogen metabolism related to temperature. In 25-325 g sea bass reared at 17°C, N excreted represented 30-58% of N ingested (Lemarié et al., 1998) and in 200g fish, at 20°C, it ranged from 34 to 47% according to feed composition (Robaina et al., 1999), but further experiments are required to determine the effects of thermal regime on N metabolism (ammonia and urea) within the concept of the energy budget. In our study, TAN excretion values were in accordance with previous findings for juvenile sea bass obtained at 17-23 °C in laboratory studies (Guérin-Ancey, 1976; Dosdat et al., 1996; Ballestrazzi et al., 1998) and on farms (Lemarié et al., 1998). MO_2R measured at

22°C was also in agreement with data from previous laboratory studies on juvenile sea bass (Claireaux and Lagardère, 1999; Pichavant et al., 2001).

This study demonstrated the temperature dependence of a Western Mediterranean population of European sea bass during on-growing when feeding and oxygen supply were not restricted. Temperature for maximum response differed depending on the variable tested: temperature for maximum feed conversion efficiency was lower than the temperature at which growth was maximum, which, in turn, was lower than the temperature at which feed intake peaked. The study also revealed a capacity for this population to adapt to high temperatures and provided some evidence that the upper temperature for growth of juveniles was close to 29°C. Given this finding a comparison of the thermal responses of populations from different geographic regions will be of interest both from a scientific and practical point of view.

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