

Effect of temperature on growth performance of greater amberjack (*SERIOLA DUMERILI* Risso 1810) Juveniles

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Abstract

In order to successfully diversify Mediterranean aquaculture, it is necessary to determine optimum culture conditions of potential candidate species such as greater amberjack (*Seriola dumerili*). Among culture conditions, rearing temperature is a key factor for achieving optimum growth and maintaining fish welfare. However, little is known about the optimum culture conditions of greater amberjack (*Seriola dumerili*). Thus, the aim of this study was to determine the effect of three different rearing temperatures (17, 22 and 26°C) during 120 days on growth performance, body morphometry, biochemical composition, gut transit and liver morphology of greater amberjack (*Seriola dumerili*) juveniles. After 120 days of rearing, fish raised at 26°C showed higher ($p < .05$) body weight and specific growth rate than fish held at lower temperatures, as well as improved feed utilization, protein efficiency and nutrient retention percentages. Fish stomach emptying was faster ($p < .05$) in fish raised at 26°C than in fish held at 22°C and 17°C. Similar results were obtained for gut transit time, being gut emptying faster ($p < .05$) in fish reared at 26°C than in fish cultured at lower temperatures. Rearing temperature also induced changes in fish morphology which resulted in a higher ($p < .05$) caudal propulsion efficiency index for fish reared at 26°C. Based on these results, we conclude that greater amberjack fingerlings perform better at 26°C than at 22°C or 17°C.

KEYWORDS

feed efficiency, gastric evacuation, greater amberjack, gut transit, morphometric analyses, rearing temperature, *Seriola dumerili*

1 | INTRODUCTION

The importance of *Seriola* spp. for the aquaculture industry is increasing worldwide (Sicuro & Luzzana, 2016). Species such as greater amberjack (*Seriola dumerili*), Japanese amberjack (*S. quinqueradiata*), long fin yellowtail (*S. rivoliana*) and the yellowtail kingfish (*S. lalandi*) are fast-growing species of special interest as candidates for marine aquaculture diversification (Hutson, Ernst & Whittington, 2007; Moran, Pether & Lee, 2009; Sicuro & Luzzana, 2016;

Takakuwa, Fukada, Hosokawa & Masumoto, 2006). Particularly, greater amberjack has a circumglobal distribution adapting to a wide temperature range varying from 15 to 27°C (Nakada, 2000) and it has been described to reach 6 kg in 2.5 years under culture conditions (Mazzola, Favalaro & Sara, 2000). However, greater amberjack aquaculture production on sea cages is limited by several bottlenecks related to monogenean ectoparasites incidence (Hirayama, Kawano & Hirazawa, 2009; Ogawa, Fukudome & Wakabayashi, 1995; Repullés-Albelda, Kostadinova, Raga & Montero, 2013). To reduce

parasite incidence, new methods for optimizing greater amberjack culture conditions have been proposed recently, such as increasing the depth of the cages (Shirakashi, Hirano, Ishitani & Ishimaru, 2013) or the utilization of inland recirculating aquaculture systems (Abbink et al., 2012), which in turn make it necessary to define the optimum culture conditions for this species for achieving maximum growth and optimum feed utilization.

As it is well known, temperature is a key factor for achieving optimum fish growth (Ibarz et al., 2010) and maintaining fish welfare (Rotllant & Balm, 2000). Indeed, inadequate temperature markedly reduces feed utilization by impaired nutrient retention (Besson, Komen, Aubin, Poelman & Arendonk, 2014; Moreira, Peres, Couto, Enes & Oliva-Teles, 2008) and causes abnormal lipid accumulation in the liver (Person-Le Ruyet, Mahé, Le Bayon & Le Delliou, 2004). Besides, increased temperature raises feed intake (Booth, Allan & Pirozzi, 2010) in relation to an increased metabolic rate or to a reduced gut transit time by increased gut motility (Jobling, 1980). Temperature is also known to induce changes in swimming efficiency (Dabrowski, Kok & Takashima, 1986; Herbing, 2002) what could be related to body shape changes (Elliott, Haskard & Koslow, 1995). Indeed, 26.5°C has been determined as optimum rearing temperature for 4-g yellowtail kingfish juveniles after 32 days of feeding based on optimized feed:gain ratio and improved growth performance (Abbink et al., 2012) in agreement with studies in other fish species, in which this parameter increased at species-specific-appropriate rearing temperatures.

Although the optimum ratio digestible protein/digestible energy has been determined for greater amberjack fingerlings held from 26 to 29°C (Takakuwa et al., 2006), little is known about the optimum temperature for this species during the on-growing phase and different rearing temperatures. Thus, the objective of this study was to determine the effects of three different rearing temperatures (17, 22 and 26°C) on growth performance, body morphometry, biochemical composition, gut transit time and liver morphology of greater amberjack (*Seriola dumerili*) juveniles.

2 | MATERIALS AND METHODS

This study was conducted at the marine biosecurity station (MBS) of the Scientific and Technologic Park of the University of Las Palmas de Gran Canaria (Las Palmas, Canary Islands, Spain). The animal experiments described comply with the guidelines of the European Union Council (2010/63/EU) for the use of experimental animals and have been approved by the Bioethical Committee of the University of Las Palmas de Gran Canaria. For the whole trial, a tank is considered as an experimental unit ($n = 3$).

2.1 | Experimental fish and experimental conditions

Two hundred and twenty-five greater amberjack juveniles of 19.5 ± 4.1 g body weight and 9.8 ± 0.7 cm total body length previously acclimatized in rearing tanks at 21°C (± 0.6) were distributed in

nine cylindrical-conical 500-l tanks (25 individuals per tank). Afterwards, three temperature treatments, at 17, 22 and 26°C (± 0.5) in triplicate, were assayed; each three tanks for a given temperature were controlled by one recirculation system. The acclimation to the experimental temperatures was conducted by increasing or decreasing temperature at a rate of 0.5°C every 3 hr, reaching experimental temperatures in 24 hr. Oxygen level was similar for each temperature, 8.0 ± 0.2 , 7.5 ± 0.6 and 7.4 ± 0.7 (17, 22 and 26°C respectively). Fish were fed to apparent satiety three times per day by hand during 120 days with a commercial diet (Europa 22, Skretting, Burgos, Spain) with 52% of crude protein and 20% crude lipids that was used for the whole trial.

2.2 | Sampling procedures

For initial sampling, three fish from each tank ($n = 3$, in triplicate for each experimental temperature) were sacrificed with anaesthetic clove oil overdose for biochemical whole body composition analyses. The same was conducted for another three fish from each tank ($n = 3$, in triplicate for each experimental temperature) for liver biochemical composition, all pooled by tank, starting the trial with 25 fish per tank. Fish weight and length were recorded every 30 days, and feed intake was recorded daily. Three fish from each tank ($n = 3$ in triplicate for each experimental temperature) were used at the end of the trial for biochemical whole body composition analyses, and other three fish ($n = 3$ in triplicate for each experimental temperature) were used to collect samples of liver for biochemical and histological analyses. All biochemical analyses were performed following standard procedures (AOAC 2000). Besides, at the end of the feeding period, all fish were photographed individually for morphometric analysis on a white background with a scale. The rest of the animals were used for a gastric evacuation time assay. For that purpose, 18 fish per tank were kept fasted during 48 hr and then fed until apparent satiation. Then, 2, 4, 8, 12, 18, 24 and 30 hr after feeding fish were sacrificed by an anaesthetic overdose (three fish in each sampling point of each tank) and stomach and intestine dissected and weighed. Intestinal and stomach content was calculated by weighing the feed content in both stomach and intestine after drying at 40°C. Data were expressed as mg of meal dry weight per 100 g of fish.

2.3 | Fish growth measurements

Condition factor (K-factor) was calculated as $100 \times (\text{final fish weight}/(\text{final length})^3)$. Specific growth rate (SGR) and feed conversion ratio (FCR) were calculated as follows: $\text{SGR} = (\text{Ln}(\text{final weight}) - \text{Ln}(\text{initial weight})) \times 100 / \text{feeding time (days)}$ and $\text{FCR} = (\text{total feed fed} / \text{total weight gained})$. The thermal growth coefficient (TGC) was calculated as follows: $(\text{final weight}^{1/3} - \text{initial weight}^{1/3}) \times 1000 / \text{daily temperature}$. The daily nutrient gain (g/kg ABW/day) was calculated as follows: $(\text{final body nutrient content} - \text{initial body nutrient content}) \times \text{ABW}^{-1} \times \text{day}^{-1}$, where ABW (average of body weight) was calculated as follows: $(W1 + W0) / 2$. Nutrient retention

(%) was calculated as (final body nutrient content – initial body nutrient content) \times N intake fish⁻¹ \times 100. The protein efficiency ratio (PER) was calculated as weight gain (g)/protein ingested (g). Hepatosomatic Index (HSI) was calculated as (liver weight (g)/fish weight (g)) \times 100.

2.4 | Morphological analysis

Geometric morphometric analyses were performed to investigate the influence of temperature in the development of the body shape. All experimental fish were photographed using digital cameras. The body shape of each individual was analysed using a landmark-based method (Rohlf & Marcus, 1993). Twenty homologous landmarks and two semi-landmarks on the left side of body were selected (Figure 1). The coordinates of these landmarks for each individual were acquired using the tpsDig2 software (Rohlf, 2004). A generalized Procrustes analysis (GPA) was performed (Dryden & Mardia, 1998; Rohlf & Slice, 1990) on the raw landmarks data to superimpose all specimens to a common location and remove the effects of size and orientation from landmark coordinates. TPS Small 1.28 software package (Rohlf, 2002) was used to evaluate the approximation of the distribution of the specimens in the Kendall's shape space relative to the linear tangent space for each analysed view (Dryden &

Mardia, 1998). The correlation coefficient between tangent distances and the Procrustes distances was high ($r = 1$), indicating that the amount of shape variation was small enough to permit statistical analyses using only the Procrustes distances. Moreover, the arching effect was removed using the Burnaby's orthogonal projection (Alós, Palmer, Linde-Medina & Arlinghaus, 2014; Valentin, Penin, Chanut, Séigny & Rohlf, 2008).

A subsample of 10 individuals was selected for each temperature to estimate the caudal propulsion efficiency through reduction of drag (CPE) (Webb, 1984). It was defined as the relation between caudal fin depth (CFd) and caudal peduncle minimal depth (CPd) (Figure 1).

2.5 | Biochemical analyses

At the end of the trial, three fish per tank (in triplicate for each experimental temperature) were collected for biochemical analyses. Samples were homogenized (T25 Digital Ultra-turrax, IKA®, Germany) pooling all animals from each tank. Each pool of samples was analysed in triplicate (triplicate for each experimental temperature) for whole body and liver composition. Ash content was determined by combustion in a muffle furnace at 600°C for 12 hr, moisture content was determined after drying at 105°C to constant weight, crude protein was determined by acid digestion using Kjeldahl method (nitrogen \times 6.25), and crude lipid was extracted following Folch, Lees and Sloane Stanley (1957) method.

2.6 | Histological analyses

Tissue samples from three fish per tank (triplicate for each experimental temperature) were fixed in 4% buffered formalin for 2 days, dehydrated in a graded series of alcohol followed by one of xylene and finally embedded in paraffin wax. Three serial sections (4 μ m) were then cut from each paraffin-embedded sample, and each processed for haematoxylin and eosin (H&E) (Martoja & Martoja-Pierson, 1970) and analysed by optical microscopy.

2.7 | Statistical analyses

For morphological analyses, the size measure of a landmark configuration called "centroid size" was computed for each image as the square root of the sum of squared distances of a set of landmarks from their centroid (Frost, Marcus, Bookstein, Reddy & Delson, 2003). Significance was evaluated using a permutation test against the null hypothesis of independence (10,000 iterations). A principal component analysis (PCA) was performed on the Procrustes coordinates to determine how the shape varied among groups. The resulting PCs are often termed "relative warps" (RWs). This is mathematically equivalent to computing a PCA using the Procrustes coordinates of each specimen after GPA when $a = 0$ (Rohlf & Marcus, 1993). The changes related to size were made by multivariate regression of the PC scores of the Procrustes coordinates (dependent variables) on fish size (independent variable). All data were

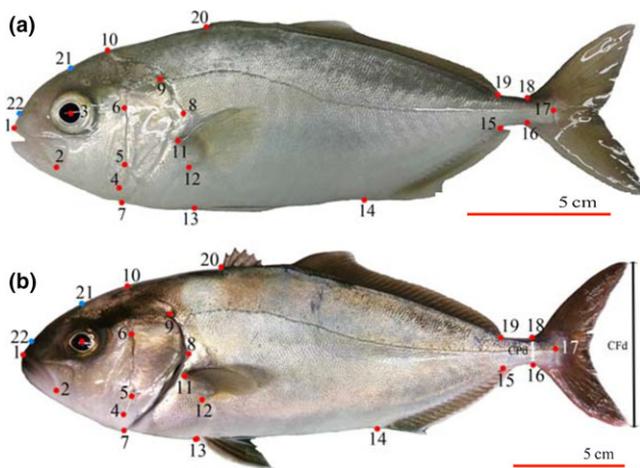


FIGURE 1 Position and meaning of landmarks (red) and semi-landmarks (blue) in body of greater amberjack reared at 17°C (a) and 26°C (b): one anterior tip of the snout; two most posterior point of the premaxilla; three midpoint of eye; four ventral elbow of interoperculum; five the point where pre-interoperculum and subinteroperculum get in contact; six dorsal end of the pre-interopercular groove; seven ventral point of the operculum; eight limit posterior of the operculum; nine limit dorsal of the operculum; 10 dorsal margin of head directly above; 11 and 12 upper and lower insertion of the pelvic fin; 13 insertion of the ventral fin; 14 and 15 anterior and posterior insertion of the anal fin; 16 and 18 lower and upper insertion of caudal fin; 17 insertion of lateral line with midpoint of the hypural notch; 19 posterior insertion of the second dorsal fin; 20 anterior insertion of the first dorsal fin; 21 dorsal projection of eye; 22 anterior projection of eye. CFd caudal fin depth; CPd caudal peduncle minimal depth.

processed with the MorphoJ ver. 1.06d (Klingenberg, 2011) and PAST ver. 3.07 (Hammer, Harper & Ryan, 2001) software packages. As the groups showed significant differences in the furcal length (ANOVA, $F = 665$, $p < .0001$), a regression between natural logarithmic of furcal length and centroid size was performed (Singleton, 2002) to examine the size effect on shape.

The rest of the data were tested for normality and homogeneity of variance. Means and standard deviations (*SD*) were calculated for each parameter measured. When required, data arcsine square-root transformation was performed, particularly when data were expressed as percentage (Fowler, Cohen & Jarvis, 1998). Statistical analyses followed methods outlined by Sokal and Rohlf (1995). A one-way ANOVA test was conducted to analyse the effects of the temperature on growth performance and biochemical analyses. Two-way ANOVA was performed to analyse the effect of temperature, time and the combine effect of both parameters on gut transit time and gastric evacuation. A Kruskal–Wallis test was used to compare

the CPE mean among the three groups followed by Dunnett's multiple comparison test. Significant differences were considered for $p < .05$. Analyses were performed using the SPSS Statistical Software System v20.0 (SPSS, Chicago, IL, USA) and R (version 3.1.0).

3 | RESULTS

3.1 | Growth performance

After 30 days of feeding, growth performance differed between fish held at 17°C and any other temperatures ($p < .05$). From 90 to 120 days of feeding, fish held at 26°C showed higher ($p < .05$) body weight than fish held at 22°C. After 60 days of trial, fish held at 17°C showed the lowest ($p < .05$) final body weight compared to fish reared at higher temperatures (Table 1). Similar results were obtained for specific growth rate (SGR) (Table 1), which registered the lowest values in fish held at 17°C. In terms of fish length, there

TABLE 1 Effect of rearing temperature on selected growth performance, feed utilization and biochemical parameters

	17°C	22°C	26°C
Fish body weight (g)			
Initial weight	19.5 ± 4.8	20.3 ± 4.9	19.3 ± 4.5
30 days	45.5 ± 7.6 ^a	77.7 ± 13.8 ^b	81.1 ± 17.3 ^b
60 days	61.7 ± 10.8 ^a	133.4 ± 22.2 ^b	141.2 ± 26.2 ^b
90 days	84.4 ± 12.1 ^a	182.5 ± 31.0 ^b	246 ± 49.5 ^c
120 days	106.4 ± 18.9 ^a	287.7 ± 45.4 ^b	384.2 ± 79.8 ^c
Final furcal length (cm)	15.6 ± 0.8 ^a	21.3 ± 1.1 ^b	22.9 ± 1.5 ^b
K-Factor	2.3 ± 0.1 ^a	2.0 ± 0.2 ^b	2.0 ± 0.1 ^b
SGR (%)	1.2 ± 0.1 ^a	1.8 ± 0.1 ^b	2.0 ± 0.1 ^c
TGC	1.1 ± 0.0 ^a	1.5 ± 0.1 ^b	1.5 ± 0.1 ^b
FCR			
30 days	0.95 ± 0.04 ^a	0.87 ± 0.06 ^{ab}	0.86 ± 0.04 ^b
60 days	1.57 ± 0.13 ^a	1.08 ± 0.07 ^b	1.14 ± 0.09 ^b
90 days	1.42 ± 0.21 ^a	1.07 ± 0.03 ^b	1.06 ± 0.08 ^b
120 days	1.42 ± 0.30 ^a	1.14 ± 0.10 ^{ab}	1.01 ± 0.08 ^b
Total	1.35 ± 0.09 ^a	1.04 ± 0.06 ^b	1.01 ± 0.04 ^b
Feed intake (g feed/fish/day)	1.0 ± 0.0 ^a	2.6 ± 0.1 ^b	3.1 ± 0.0 ^c
HSI (%)	1.51 ± 0.18 ^a	1.28 ± 0.16 ^b	1.09 ± 0.15 ^c
Whole body proximal composition (% DM)			
Final crude lipids	30.6 ± 0.1 ^a	29.3 ± 0.1 ^b	29.1 ± 0.7 ^b
Final crude proteins	57.4 ± 0.5 ^a	55.7 ± 0.4 ^b	54.9 ± 1.7 ^b
Final moisture	71.9 ± 0.7	71.4 ± 0.9	68.8 ± 1.6
Protein retention	19.6 ± 1.5 ^a	22.3 ± 1.6 ^b	25.5 ± 0.1 ^c
Lipid retention	30.2 ± 1.7 ^a	31.9 ± 1.9 ^a	36.3 ± 1.0 ^b
PER	1.4 ± 0.1 ^a	1.6 ± 0.1 ^{ab}	1.9 ± 0.1 ^b
Liver proximal composition(% DM)			
Crude lipids	52.8 ± 1.2 ^a	37.3 ± 0.5 ^b	37.5 ± 0.4 ^b
Crude proteins	30.4 ± 0.5 ^a	34.1 ± 0.3 ^b	34.1 ± 0.7 ^b

Different letters within a row denote significant differences ($p < .05$). Initial whole body proximal composition: crude lipids: 20.0 ± 0.6; crude protein: 64.3 ± 1.0; moisture: 74.9 ± 0.9. SGR: specific growth rate; TGC: thermal growth coefficient; FCR: food conversion ratio; PER: protein efficiency ratio.

were no significant differences between fish held at 22°C and 26°C, and both groups of animals were significantly ($p < .05$) longer than those reared at 17°C after 120 days of feeding.

3.2 | Feed utilization

After 30 days of feeding trial, fish reared at 17°C presented higher FCR ($p < .05$) than fish held at 26°C, but similar to that of fish cultured at 22°C (Table 1). After 60 and 90 days of feeding, fish held at 17°C also presented the highest ($p < .05$) FCR in relation to fish reared at higher water temperatures (Table 1). Regarding total FCR for the whole on-growing period, fish held at 26°C showed the lowest ($p < .05$) FCR, being this value below one (Table 1), and fish held at 22°C presented significant ($p < .05$) lower FCR when compared with those held at 17°C. The voluntary feed intake referred to g of feed/fish/day denoted significant differences among temperatures increasing with temperature (Table 1). Hepatosomatic Index (HSI) showed significant differences among temperatures ($p < .05$), decreasing the value with increasing temperature (Table 1).

Whole body biochemical analyses showed differences among temperatures in lipids and proteins (%DM) (Table 1). The protein retention and lipid retention were higher ($p < .05$) for fish held at 26°C compared to the rest of the rearing temperatures (Table 1). Fish reared at 17°C presented significantly higher ($p < .05$) liver lipid content and lower protein content when compared with fish held at higher water temperatures (22 and 26°C).

3.3 | Morphology of fish body

Significant differences among groups were found in the centroid size (ANOVA procrustes, $F = 6.85$, $p = .0014$) and shape ($F = 8.79$, $p < .0001$). The centroid size was correlated with fish length ($p = .0005$), explaining the 7.65% of variation for allometry accounts, which indicated a change shape linked to fish growth. The PC1 (RW1) attained 21.6% of variance and it was strongly related to fish size ($r = -.500$; $p < .0001$), whilst PC2 (RW2)

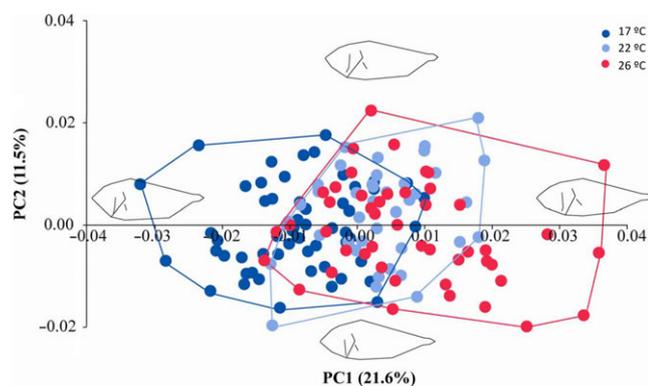


FIGURE 2 Scatter plot of the PCA components 1 and 2 (PC1 and PC2) of the body shape of greater amberjack reared at different temperatures. Illustration indicates shape changes (negative and positive) using warped outline drawing.

described 11.5% of variability and it was not correlated with fish size ($r = -.017$, $p = .837$). The PC1 indicated that the increase in temperature led to elongated shape of fish body, especially of the head (Figure 2), differentiating clearly the specimens reared between 17°C and 26°C. However, PC2 did not have the same consistency with the temperature, and all individuals presented similar morphological variability.

The mean values of caudal propulsion efficiency (CPE) differed among the groups (K-S statistic = 16.34, $p < .001$), noting higher propulsion of fish with a temperature increase (Figure 3). The specimens reared at 26°C showed significant swimming differences with the individuals cultivated to 17°C (Dunn's Z-statistics = -15.7 , $p < .001$) and 22°C (Dunn's Z-statistics = -10.1 , $p < .05$), whilst it was similar between the individuals reared at 17°C and 22°C (Dunn's Z-statistics = -5.6 , $p > .05$).

3.4 | Liver histology

Histological results indicated a clear effect of rearing temperature on hepatocyte intracytoplasmic lipid accumulation, being reduced with increasing water temperature as shown in Figure 4. Thus, livers of fish reared at 17°C showed a high number of hepatocytes with large intracytoplasmic lipid vacuoles, displacing the nucleus to the periphery (Figure 4a), whereas livers of fish reared at 26°C presented the lowest hepatocyte intracytoplasmic lipid vacuoles, resulting in a more prominent nuclei alignment around sinusoidal spaces (Figure 4c). Livers of fish cultured at 22°C (Figure 4b) showed lower hepatocyte lipid vacuolization than fish reared at 17°C but higher than fish cultivated at 26°C.

3.5 | Gastric emptying and gut transit time

The two-way ANOVA analysis demonstrated that both gastric emptying and gut transit time are significantly ($p < .05$) affected by time, temperature and combined effect of both parameters. After 2 and

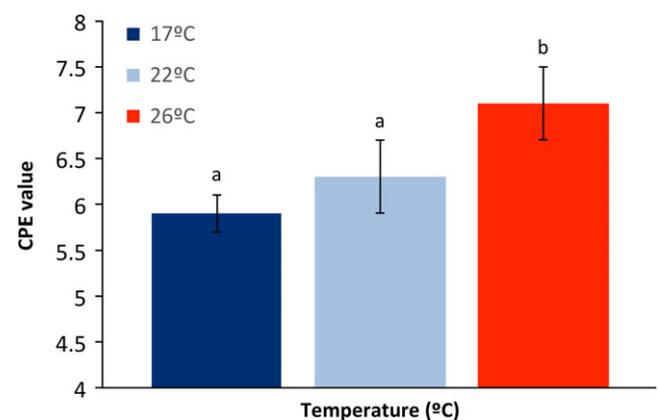


FIGURE 3 Caudal propulsion efficiency (CPE) value of greater amberjack juveniles after 120 days held at different temperatures. Relationship between caudal fin depth (CFd) and caudal peduncle minimal depth (CPd).

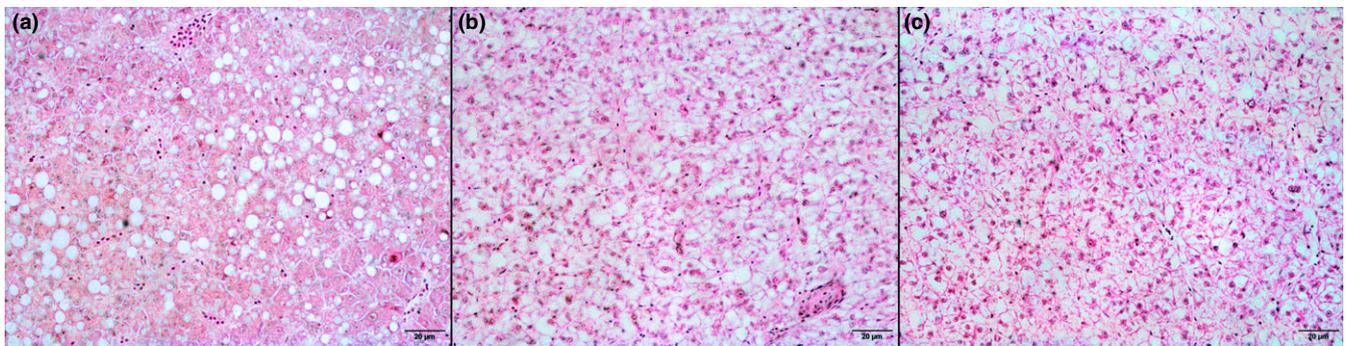


FIGURE 4 Hepatic histological samples stained with haematoxylin–eosin (H & E) from greater amberjack juveniles held at different experimental rearing temperature; A: 17°C ×40; B: 22°C ×40; C: 26°C ×40.

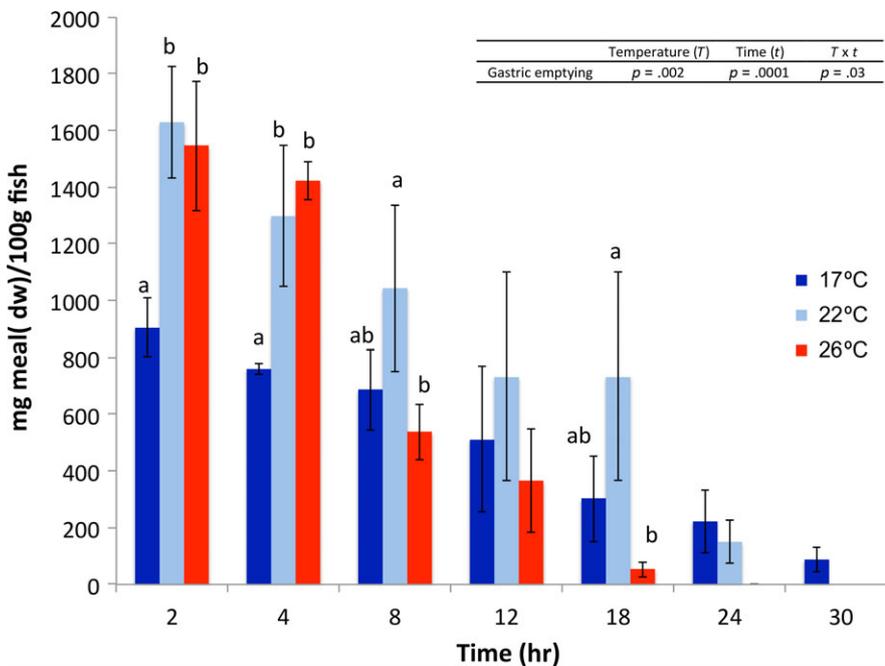


FIGURE 5 Gastric emptying time (mg meal dry weight/100 g of fish) of greater amberjack juveniles after 120 days held at different temperatures. Different letters within each sampling point denote significant differences among temperatures ($p < .05$).

4 hr post feeding, fish held at 22° and 26° C presented higher content of meal ($p < .05$) in the stomach compared to those fish reared at 17°C. However, after 8 hr of feeding the gastric content of fish held at 26°C decreased significantly ($p < .05$) compared to fish reared at 22°C, whereas no differences were detected when compared with fish reared at 17°C. This pattern was constant in time until 18 hr after feeding, when fish held at 26°C presented an almost empty stomach and no gastric content 24 hr after feeding. This gastric emptying time contrast with those fish held at 22°C which still presented gastric content after 24 hr and to those held at 17°C that showed gastric content even after 30 hr of feeding (Figure 5).

In general terms, fish held at 26°C showed the faster gastric emptying when compared with fish held at lower water temperatures (Figure 5). Similar results were obtained for gut transit time; indeed, fish held at 17°C and 22°C presented similar gut content along the experimental period with exception of 12 and 18 hr post feeding (Figure 6).

4 | DISCUSSION

In the present study, rearing temperature affected fish growth, where greater amberjack held at 22°C showed a significant ($p < .05$) lower growth rate than at 26°C. Temperature is an important factor affecting the growth performance of fish (Brett, 1979) and the nutrient utilization efficiency (Peres & Oliva-Teles, 1999). Variations in rearing temperature have been described to induce modifications on growth rate, feed intake, feed conversion efficiency and stomach evacuation rate in several cultured species such as Atlantic salmon (*Salmo salar*) (Handeland, Imsland & Stefansson, 2008) or European sea bass (*Dicentrarchus labrax*) (Person-Le Ruyet et al., 2004). Fish growth rate is highly temperature dependent (Pérez-Casanova, Lall & Gamperl, 2009; Van Ham et al., 2003), depending not only on the amount of feed ingested but also on the efficiency in which fish convert feed to weight gain (Handeland et al., 2008), which at the same time is fish species specific. Similarly, low rearing temperature (2°C)

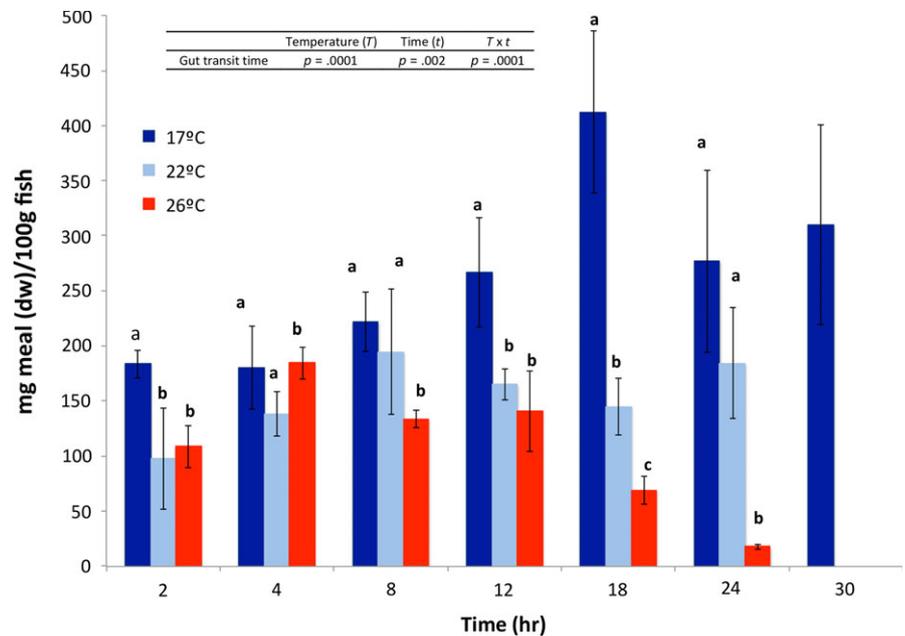


FIGURE 6 Gut transit time (mg meal dry weight/100 g of fish) of greater amberjack juveniles after 120 days held at different temperatures. Different letters within each sampling point denote significant differences among temperatures ($p < .05$).

reduced dramatically SGR and food consumption in Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) when compared with fish reared at 11°C (Pérez-Casanova et al., 2009). On one hand, the decrease in Atlantic cod growth rate has been found to be directly related to lower feed intake. On the other hand, the reduction in haddock growth rate was found to be associated with reduction in both feed intake and gross conversion efficiency.

The better rearing temperature in terms of achieving better fish growth performance has been studied in several fish species of great interest for aquaculture, including turbot (*Scophthalmus maximus*) (Imsland et al., 2001; Van Ham et al., 2003), Atlantic cod (Björnsson, Steinarsson & Oddgeirsson, 2001), European sea bass (Person-Le Ruyet et al., 2004) or Atlantic salmon (Handeland et al., 2008). However, information about optimum growth temperature in warm-water fast-growing species is scarce. In agreement with the results obtained in the present study after 30 days of feeding, yellowtail kingfish reared at 18°C showed a reduced growth compared with fish held at 22°C (Bowyer, Qin, Smullen & Stone, 2012). Besides, for the same species, an increasing water temperature from 21°C up to 26.5°C for 32 days resulted in a 54% improvement in relative growth (Abbink et al., 2012). Similarly, in the present experiment, there was also a 35% increase in weight gain with the elevation of water temperature from 22°C up to 26°C, in agreement with previous studies in other fish species (Abbink et al., 2012; Bowyer et al., 2012; Collins, Ball, Qin, Bowyer & Stone, 2014).

Besides, optimum temperature may vary depending on the variable evaluated. For example, for European sea bass, Person-Le Ruyet et al. (2004) described different optimum rearing temperature value depending on achieving maximum feed conversion efficiency or weight gain, as described also for Atlantic salmon post-smolts (Handeland et al., 2008) as follows: $FCR < \text{growth} < \text{feed intake}$, as previously proposed by Jobling (1994) who postulated that when fish were fed at unrestricted ration growth rate reaches its maximum at a lower temperature than that needed for achieving maximum

ingestion rate. However, studies in other species such as rainbow trout (*Oncorhynchus mykiss*) (Bailey & Alanärä, 2006), hapuku (*Polyprion oxygeneios*) (Khan, Pether, Bruce, Walker & Herbert, 2014, 2015), dusky kob (*Argyrosomus japonicus*) (Collett, Vine, Kaiser & Baxter, 2008), turbot (Árnason, Björnsson, Steinarsson & Oddgeirsson, 2009; Van Ham et al., 2003) striped bass (*Morone saxatilis*) (Duston, Astatkie & Maclsaac, 2004) and some species of the genus *Seriola* (Abbink et al., 2012; Bowyer et al., 2014) achieve their optimum FCR at the same temperature as optimum growth in agreement with the results obtained in the present study.

FCR values obtained within the present study correspond to those described for other fast-growing species such as meagre or kingfish yellowtail (Abbink et al., 2012; Chatzifotis, Panagiotidou & Divanach, 2012) and some other fish species such as rainbow trout, eel (*Anguilla sp.*), barramundi (*Lates calcarifer*), Atlantic cod, turbot, tilapia and Japanese yellowtail (included in Tacon & Metian, 2008). Indeed, the lower FCR found for greater amberjack held at 26°C could be related to a higher protease activity and subsequently better protein digestibility (Abbink et al., 2012; Kofuji, Akimoto, Hosokawa & Masumoto, 2005), as digestive enzymes activity is directly related to temperature (Bowyer et al., 2014; Golovanova, Golovanov, Smirnov & Pavlov, 2013). A better protein retention for rainbow trout held at higher temperatures as been related to an improvement of the diet digestibility (Oliva-Teles & Rodrigues, 1993). This effect seems to be more marked in high-energy-demand and high-performance species, which have a narrow optimum temperature range for best metabolic function as temperate pelagic species (Pirozzi & Booth, 2009). Whilst there was little difference in apparent protein digestibility of Japanese yellowtail fed diets of differing protein content at 22–25°C, at 16–18°C the fish could not easily digest lower protein diets (43% protein) compared with higher protein ones (45% protein) (Kofuji et al., 2005). Also, the apparent protein digestibility of Japanese yellowtail fed single moist pellets decreased from 84 to 69% when the water temperature decreased from 25°C to 14°C

(Satoh, Kimoto & Hitaka, 2004). In the present study, temperature affected the metabolism of other main nutrients increasing lipid retention with increasing rearing temperatures, in agreement with previous studies in other fish species such as blue gourami (*Trichogaster trichopterus*) (Mohanta, Subramanian & Korikanthimath, 2013) and Ussuri catfish (*Pseudobagrus ussuriensis*) (Wang et al., 2013).

In the present study, fish held at 17°C showed an altered liver morphological pattern characterized by a high hepatocyte intracytoplasmic lipid accumulation compared to fish held at higher rearing temperatures. At the same time, this morphological pattern is directly related to the higher lipid liver content and HSI found in fish held at 17°C. Altogether denoting a clear effect of rearing temperature on lipid metabolism for this fish species as described before for other fish species which also presented (Person-Le Ruyet et al., 2004). Indeed, decreasing temperature produces a mobilization of lipids from muscle and perivisceral regions to liver, whereas increasing temperature induces a greater metabolic activation that leads to a higher lipid mobilization from the liver (Ibarz et al., 2007). Furthermore, in gilthead sea bream (*Sparus aurata*) low temperatures induce an increase in HSI due to a higher mobilization of lipids as a result of an increased energy demand caused by the adaptation to thermal changes (Ibarz et al., 2007) as detected in the present study for fish held 17°C. In this regard, the effect of temperature on fish metabolism seems to be tissue specific as described in cold acclimated carp (*Cyprinus carpio*), in which a divergent energetic and metabolic strategies among tissues were described, with modulates brain glycolytic activity, and liver showing a transition to lipid metabolism and remodels muscle contractile apparatus (Gracey et al., 2004). Besides, temperature has been also shown to exert a positive effect on the expression of growth factor genes in the liver of different species, such as Nile tilapia (*Oreochromis niloticus*) (Vera Cruz et al., 2006) or kingfish yellowtail (Collins et al., 2014). This effect of lower temperatures in feed efficiency and the metabolic pathways involved seems to be even more marked in high-energy-demand and high-performance species, such as temperate pelagic species, which have a narrow optimum temperature range for best metabolic function (Pirozzi & Booth, 2009).

Fish gut transit time and gastric emptying have been described to be highly dependent on water temperature (Gräns, Albertsson, Axelsson & Olsson, 2009; Handeland et al., 2008; Jobling, 1980; Miegel, Pain, van Wettere, Howarth & Stone, 2010; Specziar, 2002). Higher temperature reduces time of the gastric emptying, what is important to prevent a possible gastric overload resulted in a reduced absorption efficiency (Riche, Haley, Oetker, Garbrecht & Garling, 2004). In this regard, in the present study for fish held at 17°C, it took twelve hours more to evacuate intestinal content than for fish held at 26°C in agreement with previous results in other *Seriola* species. For instance, in yellowtail kingfish gut transit time was triplicated in winter (around 12°C) compared to summer (around 20°C) (Miegel et al., 2010). This is also consistent with previous studies in Japanese yellowtail (Nakada, 2000; Watanabe et al., 2001)

where water temperature has been shown to accelerate stomach evacuation and gut transit time. Gastric emptying depends primarily on water temperature, being the amount of consumed food a secondary factor (Kawaguchi, Miyasaka & Genkai-Kato, 2007) and changes in gastric emptying rate usually are more evident at low temperatures (Handeland et al., 2008). For example, variations on gastric emptying rate were more evident in Atlantic salmon between the lowest temperature assayed (6°C) and the other three temperatures assayed (10°C, 14°C and 18°C) that showed similar gastric emptying ratio (Handeland et al., 2008). The results of the present experiment are in agreement with this, as evacuation rates stabilize nearer the upper thermal tolerance limit of a given species (Sweka, Cox & Hartman, 2004).

Apart from the differences obtained in feed utilization and growth performance, different temperatures induced important modifications in fish body shape. Morphology plasticity may have important consequences for fish production, as it affects growth, size and time of reproduction (Ohlberger, Staaks & Hölker, 2006). Fish reared at 26°C presented a body elongation providing a silhouette similar to wild fish, whereas fish reared at 17°C showed a more rounded head. Although alterations of head shape can be related to deformities (Berillis, 2015), no deformed animals were observed in the present study. Furthermore, morphometric analyses showed higher caudal propulsion efficiency index (CPE) in fish held at 26°C, which predicts improved movement efficiency during swimming (Webb, 1984). Changes produced in the body shape of the fish become more important in pelagic fish exposed to high water current than in benthonic species (Meyers & Belk, 2014). Studies on the activity and associated energetics of actively swimming fish have shown that less efficient movements require higher oxygen consumption (Gleiss, Dale, Holland & Wilson, 2010), what could be partially related to differences in feed efficiency (Kawabe et al., 2003). Therefore, morphological variations related to temperature increase up to 26°C would predict improved swimming and feeding efficiencies (Azaza, Dhraïef & Kraïem, 2008; Khan et al., 2014) in a synergistic mode with feed utilization and growth.

In summary, the best growth and feed utilization was obtained when greater amberjack juveniles (20 g initial body weight) were reared at 26°C. The best growth was also associated with the best-feed efficiency and feed consumption and induced a positive effect on fish morphology. At that temperature, nutrient retention and both gastric emptying and gut transit time were also improved.

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