Latin American Journal of Aquatic Research, 49(2): 258-271, 2021
DOI: 10.3856/vol49-issue2-fulltext-2563

Research Article

Growth, thermal preference and critical thermal maximum for *Totoaba macdonaldi*: effect of acclimation temperature and inclusion of soybean meal in the diet

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ABSTRACT. We studied the interaction effect between temperature 23 and 26°C, and replacing fishmeal for soybean meal (SBM): 32, 43, and 56% *vs*. a diet control on culture performance, thermal behavior, and critical thermal maximum (CTMax) of juvenile *Totoaba macdonaldi*. Fish were fed to apparent satiation three times daily for 61 days. The results showed that temperature had a significant effect ($P < 0.05$) on weight gain, percent weight gain, and specific growth rate, which were all higher in fish acclimated at 26°C. The preferred temperature ranged between 26.4 and 27.7°C, significantly influenced by acclimation temperature ($P < 0.05$) but not by diet. CTMax was influenced by acclimation temperature and SBM in the diet. Fish resistance decreased when the percent SBM in the diet was higher. Information on biological indicators for *T. macdonaldi* adds to the knowledge of a key Mexican species. Our study demonstrated that the use of SBM as an alternative to fishmeal in the diet and the interaction with temperature as a factor could affect this species' performance.

Keywords: *Totoaba macdonaldi*; acclimation temperature; soybean meal; growth; thermal biology

INTRODUCTION

Totoaba macdonaldi overfishing and habitat degradation of areas for breeding and spawning lead to depleting its natural stocks. This species is currently protected by a fishery moratorium issued by the Mexican government in 1975 (Flanagan & Hendrickson 1976) and, since 1976, it has been listed in the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES) Appendix I as threatened with extinction, and its international trade is prohibited (Findley 2010). Through hatcheries set up as Environmental Management Units for Wildlife Conservation (UMA, for its acronym in Spanish), totoaba is being bred in captivity for use repopulation, aquaculture research, and establishment of responsible commercial fisheries (www.iaes.gob.mx).

Totoaba (*T. macdonaldi*) is a species endemic to the Gulf of California (Flanagan & Hendrickson 1976) that is considered to have aquaculture potential (Rueda-López et al. 2011). Recent studies have evaluated its nutritional requirements (Badillo-Zapata et al. 2016, Barreto-Curiel et al. 2018, Fuentes-Quesada et al. 2018, Mata-Sotres et al. 2018). However, no studies have addressed the effect of the thermal conditions, particularly the interaction between temperature and diet, on its biological performance.

Temperature is considered the abiotic factor that most strongly influences aquatic organisms' biology and physiology (Beitinger & Lutterschmidt 2011). Its effects on survival, growth (Morgan & Metcalfe 2001), behavior (Pulgar et al. 2003), and physiological capacity (Pörtner 2001, Clark et al. 2013) are well documented. Simultaneously, the energy content of

Corresponding editor: Alvaro Bicudo

food influences body temperature and metabolism (Guillaume et al. 2004).

Fish have developed the ability to respond to temperature variations by choosing thermal regions through behavioral thermoregulation (Bicego et al. 2007, Angilletta 2009). The temperature preferred by organisms is usually related to the thermal range in which the physiological, biochemical, and metabolic processes are more efficient (Beitinger & Fitzpatrick 1979). Other responses of fish to temperature include thermal tolerance and resistance. It can be determined by 1) the static method, which evaluates the incipient lower and upper lethal temperatures (Lutterschmidt & Hutchison 1997, Eme & Bennet 2009), or 2) the dynamic method, which determines the critical thermal minimum (CTMin) and maximum (CTMax) (Cowles & Bogert 1944, Bennett & Beitinger 1997, Lutterschmidt & Hutchinson 1997). Critical temperatures have been determined in fish and, since few specimens are required, they can be determined in endangered species (Gelbach et al. 1978, Lutterschmidt & Hutchinson 1997). Also, critical temperatures can be recorded experimentally in a very short time (less than two hours) and reveal biotic or abiotic factors' influence on this response (Beitinger & Lutterschmidt 2011). As critical temperatures are related to the natural environment, they have been used as indicators of stress and adaptation (Paladino et al. 1980).

Aquaculture feeds are commonly based on a fish meal (FM) due to its high protein content (Hardy 2008), the right balance of essential amino acids, high digestibility (Ayodele 2010), and high content of n-3 polyunsaturated fatty acids and other nutrients (NRC 2011a). Fishmeal is mainly obtained from pelagic fishes (Hardy & Tacon 2002), whose natural populations are now declining due to overfishing. Thus, creating the need to identify alternative protein sources for aquaculture's future development (Naylor et al. 2009, Olsen & Hasan 2012). Fishmeal is also expensive, making it unattractive for commercial aquaculture. Proteins from plant sources such as wheat, corn, pea, bean, peanut, sunflower, canola, and soy, among others (NRC 2011a), have been proposed as alternative sources since the amino acid composition of their proteins is similar to that of animal protein (Watanabe 2002). Unfortunately, these plant sources also contain other complex components that make them more difficult to assimilate than fishmeal (NRC 2011a). Therefore, the nutritional value of plant protein must be evaluated to elucidate the proportion that could be safely included in the diet (Glencross et al. 2007).

Soybean meal (SBM) is considered a high-quality protein source due to its amino acid content, making it a good fish culture option (Brown et al. 2008). SBM has been used to replace FM in fish and shrimp cultures with favorable results when percentages of up to 50% -depending on the species- have been included (Glencross et al. 2004, Kader et al. 2012). To cultivate species with aquaculture potential, such as *T. macdonaldi*, it is important first to determine their nutritional requirements so that specific diets that promote their adequate growth under different temperature conditions can be formulated (López et al. 2006, Rueda-López et al. 2011, Perez-Velazquez et al. 2016).

Both temperature and diet separately affect the biological performance of organisms. However, some studies have shown that the interaction between temperature and diet quality can produce substantially different effects. Studies conducted to determine the preferred temperature of fish indicate that acclimation temperature (Reynolds & Casterlin 1979) and diet quality (Pulgar et al. 2003, Killen 2014) significantly affect the temperature range selected. This interaction can influence food intake and, therefore, food efficiency, growth, and condition factor, among others (Eya et al. 2017).

In addition to the nutritional requirements of totoaba already reported (Badillo-Zapata et al. 2016, Perez-Velazquez et al. 2016, Barreto-Curiel et al. 2018, Fuentes-Quesada et al. 2018, Mata-Sotres et al. 2018), further research is needed on how the diet quality changes when some fraction of fishmeal is replaced by plant protein, including the interaction with thermal conditions. This study aimed to evaluate the combined effect of temperature and diet quality (i.e. varying percentages of soybean meal) on the biological performance of juvenile *T. macdonaldi* evaluated in terms of growth, thermal growth coefficient, thermal preference, and critical thermal maximum.

MATERIALS AND METHODS

Specimen collection and conditioning

Totoaba macdonaldi juveniles hatched from ovulated eggs donated by the Centro Reproductor de Especies Marinas del Estado de Sonora (CREMES) at Bahía Kino, Sonora, Mexico. Eggs were incubated at 24°C and hatched in a 1 m^3 tank in the Marine Fish Culture Laboratory of the Centro de Investigación Científica y de Educación Superior de Ensenada (CICESE). When the fish reached an average weight of 83 ± 4.2 g, they were transported at Instituto de Investigaciones Oceanológicas of the Universidad Autónoma de Baja California (IIO-UABC), and placed in two recirculation systems, each consisting of twelve 500-L plastic tanks at 24°C, before their acclimation at 23 or 26°C.

Each experimental system consisted of a 1.2 m^3 compensation tank, inside which a 7,500 W titanium heater was placed to keep the temperature constant, together with a 1/3 HP pump, a 6 ft^3 bead biofilter (PolyGeyser®, Pneumatic Drop Bead Filter model PG7 International Filter Solutions, TX, USA), and a generic 30 GPM Protein Skimmer. Each system was assigned to one of the acclimation temperatures (23 or 26°C) previously selected based on the preferred value determined for 2-month-old juvenile *T. macdonaldi* by Talamás (2001). Twelve specimens were placed in each tank, and the culture was kept under controlled conditions of dissolved oxygen (7.4 ± 0.8 mg L^{-1}), salinity (32 ± 1 g L^{-1}), pH (8 ± 0.1), and natural photoperiod (autumn season). Temperature, dissolved oxygen, and salinity were recorded daily with a multiparameter (YSI model 85-10); pH, ammonium, nitrites, nitrates, and alkalinity were measured using a commercial test kit (API® Test Kit, ApiFishcare®) at three-day intervals.

Experimental diets

Four isoproteic (50%) and isolipid (10%) diets were formulated according to the nutritional requirements of *T. macdonaldi* as determined by Rueda-López et al. (2011) (Table 1). The diets were prepared in the Laboratorio de Investigación y Desarrollo para la Acuacultura (LINDEAACUA) at IIO-UABC. In three of the diets, the main protein source, fish meal (FM), was partially replaced with varying proportions of soybean meal (SBM), as follows: diet 1 (D1): 68%FM-32%SBM, diet 2 (D2): 57%FM-43%SBM, and diet 3 (D3): 44%FM-56%SBM. Lipid concentration in the three diets was adjusted by adding fish oil in proportion to FM replacement. The fourth feed was the control diet (CD): 100%FM, which lacked SBM and had FM as the main protein source.

Proximate analysis

The four diets (control and diets with partial replacement of fishmeal with soybean meal) were determined using standard procedures (AOAC 1990); the results were expressed on a dry-matter basis. Ash content was determined by incineration of organic matter at 500°C for 24 h in a muffle (Lindberg/Blue model BF51842PBFMC-1). Moisture content was calculated from 1.0 g samples dried in the muffle to constant weight at 70°C for 24 h. Total nitrogen content (%N) was determined using the micro-Kjeldahl method, and the percentage of crude protein (CP) was calculated as %N×6.25. Total lipid content was determined after Soxhlet extraction with petroleum ether; the dissolved fat was then dried and evaluated by gravimetry. The nitrogen-free extract (NFE) was calculated using the equations proposed by Olvera-Novoa et al. (1994).

Culture conditions

All the procedures performed in this study for the experimental culture of *T. macdonaldi* followed the NRC (2011b) guidelines for ethical and responsible research.

Fish with an average weight of 83 ± 4.2 g were acclimated at either 23 or 26°C. During the first week, the fish were fed a commercial diet (Europe-Skretting 2.0 mm, 50% protein, 8% lipid) at a daily feeding rate of 3% of the average body weight, divided into three servings a day. During the second week, the commercial diet was gradually replaced (20% per day to reach 100%) with the experimental diets (CD, D1, D2, and D3).

Juvenile fish reached an average weight of 100.6 ± 0.21 g by the end of the two-week conditioning period. At that time, the experimental temperature-diet trials began. From day 1 to day 61 of culture, fish were fed the experimental diets to apparent satiation three times daily (8:00, 12:00 and 16:00 h). Any food not consumed was removed after 30 min of remaining in the water column; feces were removed daily before the first feeding and half an hour after the last feeding of the day.

All fish were measured (total length, cm) and weighed (g) at the beginning of the experimental trial and then every month for two months. The biological performance of fish was evaluated in terms of survival (%), percent weight gain (WG), specific growth rate (SGR), feed conversion ratio (FCR), and thermal growth coefficient (TGC):

$$\text{Survival} = \frac{\text{final number of fish}}{\text{initial number of fish}} \times 100$$

WG (%) = [(final average wet weight - initial average wet weight) × 100/initial average wet weight]

$$\text{SGR } (d^{-1}) = \frac{[\ln \text{final weight (g)} - \ln \text{initial weight (g)}]}{\text{days of culture}} \times 100$$

$$\text{FCR} = \frac{\text{total feed consumed (g)}}{\text{wet weight gained (g)}}$$

$$\text{TGC} = \frac{(\text{final weight (g)}^{1/3} - \text{initial weight (g)}^{1/3})}{\text{T(°C)} \times \text{days}} \times 1000$$

Preferred temperature

The system designed by Bückle et al. (2003) was used for the study of thermoregulatory behavior. This system consists of a 26 cm high, 31 cm wide and 365 cm long

Table 1. Ingredients in diets formulated (g kg^{-1}) for cultivating juvenile *Totoaba macdonaldi* at two acclimation temperatures. CD: control diet, D1: diet 1, D2: diet 2, D3: diet 3, FM: fish meal, SBM: soybean meal. Rovimix®; vitamin and mineral mix (g kg^{-1}): ρ-aminobenzoic acid 1.45; biotin 0.02; myo-inositol 14.5; nicotinic acid 2.9; Capantothenate 1.0; pyridoxine-HCl 0.17; riboflavin 0.73; thiamine-HCl 0.22; menadione 0.17; α-tocopherol 1.45; cyanocobalamin 0.0003; calciferol 0.03; L-ascorbyl-2- phosphate-Mg 0.25; folic acid 0.05; choline chloride 29.65; retinol 0.015; NaCl 1.838; $MgSO_4 \cdot 7H_2O$ 6.85; $NaH_2PO_4 \cdot 2H_2O$ 4.36; KH_2PO_4 11.99; $Ca(H_2PO_4)_2 \cdot 2H_2O$ 6.79; Fe-citrate 1.48; Ca-lactate 16.35; $AlCl_3 \cdot 6H_2O$ 0.009; $ZnSO_4 \cdot 7H_2O$ 0.17; $CuCl_2$ 0.0005; $MnSO_4 \cdot 4H_2O$ 0.04; KI 0.008; $CoCl_2$ 0.05 and Stay-C (vitamin C) donated by DSM, Nutritional Products Guadalajara, Mexico.

Ingredient	CD (100%FM)	D1 (68%FM-32%SBM)	D2 (57%FM-43%SBM)	D3 (44%FM-56%SBM)
Fish meal	620.5	424.9	355.0	272.1
Soy concentrate	0.0	100.0	100.0	100.0
Soybean meal	0.0	128.8	255	405.3
Cornmeal	171.5	117.9	53.6	0.0
Wheat flour	44.9	45.0	45.0	22.6
Lysine	0.0	1.2	1.3	1.3
Methionine	0.0	1.5	1.9	2.4
Fish oil	35.4	53.0	60.5	68.6
Taurine	10.0	10.0	10.0	10.0
Gelatin	50.0	50.0	50.0	50.0
Native starch	40.0	40.0	40.0	40.0
Rovimix®	25.0	25.0	25.0	25
Stay C	0.5	0.5	0.5	0.5
Sodium benzoate	2.0	2.0	2.0	2.0
BHT	0.1	0.1	0.1	0.1
Choline chloride	0.1	0.1	0.1	0.1
Total	1000	1000	1000	1000
Proximate composition g kg^{-1} (analyzed)				
Crude protein	484.27	486.76	490.23	487.82
Total lipids (g kg^{-1})	91.27	93.54	93.37	93.76
Nitrogen-free extract	215.21	234.82	237.56	255.04
Ash (g kg^{-1})	137.24	118.82	105.28	96.46
Energy (KJ g^{-1})	15.83	15.88	15.76	15.54
E:P ratio (mg protein KJ^{-1})	30.60	30.65	31.10	31.39

Plexiglas channel with a total capacity of 220 L, subdivided into 15 virtual chambers, each measuring 20.33 cm long. A temperature sensor connected to a multichannel thermograph (Stanford Research Systems, model SR630) was placed at the center of each virtual chamber; temperature data were sent to a printer (Panasonic KX-P3696 Multi-mode) every 10 min. Water temperature at one end of the channel was raised using two 1,000 W titanium heaters; the water at the opposite end was cooled off using a heat exchanger (Neslab Merlin M150), creating a 20-33°C thermal gradient along the channel.

The thermal preference study was carried out using four fish from each experimental unit; each time, two fish were placed in the gradient chamber corresponding to their acclimation temperature (23 or 26ºC). After a 30 min transition period, the fish's location along the channel and the chambers' temperature were recorded every 10 min for 2.5 h. All the experiments were run in triplicate, separately for each diet by temperature combination. Water was continuously injected (80 mL min^{-1}) into the system at one end of the channel to replace approximately 50% of the volume in 24 h to prevent the accumulation of metabolites.

Critical thermal maximum (CTMax)

Four fish from each experimental unit were used for the CTMax study. A single fish was placed in a 150 L plastic tank containing 60 L of water. Water temperature was increased at a constant rate of 1°C min^{-1} (Jobling 1981, Lutterschmidt & Hutchison 1997) using three 1000 W heaters attached to a diffusing stone to maintain a continuous air supply, achieve a homogeneous temperature, and avoid stratification in the water column.

As the water temperature was raised, the thermal value was recorded when the fish exhibited the loss of balance response (Lutterschmidt & Hutchison 1997, Beitinger et al. 2000). At the end of the test, the fish were killed under ethical and responsible research (NRC 2011b) guidelines.

Fish were not fed 24 h before the preferred temperature and CTMax experiments to avoid interference by post-digestion processes.

Statistical analyses

Percent values were arcsine transformed before statistical analyses. All the data were tested for normality (Kolmogorov-Smirnov, Lilliefors, and Shapiro-Wilk tests) and homogeneity of variance (Levene test). Two-way ANOVAs were carried out to evaluate the effects of acclimation temperature, experimental diets, and the interaction between the two factors. Dunnett's *post-hoc* test was used to compare each of the fishmeal-replacement treatments with the control diet. Fisher's least significant difference test was used to test for differences between the different treatments means. All the analyses were performed at a 0.05 significance level using the software Statistica 10™ (StatSoft, Inc. USA).

RESULTS

Biological performance: survival, specific growth rate, and thermal growth coefficient

A two-way ANOVA showed that neither the main factors (i.e. acclimation temperature and diet) nor their interaction significantly affected survival. A 100% survival was recorded in most treatments, except for the 23°C acclimation temperature × D1 treatment, in which a 97% survival was recorded (Table 2).

Two-way ANOVAs showed that only acclimation temperature significantly affected final average weight, percentage weight gain, and the specific growth rate. Neither diet nor the interaction between the two experimental factors had any significant effect on these variables. The highest average weight was attained by fish acclimated at 26°C fed D2 (264.17 ± 7.9 g); this was significantly higher than the average weight attained by fish acclimated at 23°C and fed D1 (230.3 ± 14 g; $P = 0.016$), D2 (223.0 ± 9.0 g; $P = 0.004$), or D3 (235.0 ± 25 g; $P = 0.34$). There were no significant differences between the SBM diets and the control diet (Table 2).

The largest average percent weight gain (155.9 ± 30%) was attained by fish acclimated at 26°C fed D3 (44%FM-56%SBM); this was significantly larger than the weight gained by fish acclimated at 23°C fed D1 (120.7 ± 15; $P = 0.024$), D2 (107.2 ± 12; $P = 0.003$) or D3 (121.6 ± 23; $P = 0.27$). There were no significant differences in percent WG between the SBM diets and the CD (139.6 ± 9% at 23°C and 137.8 ± 16% at 26°C) (Table 2).

The highest SGR (1.53 ± 0.05 d^{-1}) was observed in fish acclimated at 26°C and fed D2; this was significantly higher than the SGR recorded in fish acclimated at 23°C and fed D1 (1.31 ± 0.1; $P = 0.021$), D2 (1.25 ± 0.06; $P = 0.005$) or D3 (1.33 ± 0.17; $P = 0.035$). There were no significant differences in SGR between the SBM diets and the CD.

A two-way ANOVA showed that diet had a significant effect ($P = 0.02$) on the feed conversion ratio (FCR), but neither acclimation temperature ($P = 0.32$) nor the interaction between the two experimental factors ($P = 0.34$) had any significant effect. The FCR of fish acclimated at 23°C and fed D3 was significantly higher ($P = 0.023$) than that of fish fed CD at 23ºC. Among the SBM treatments, the lowest average FCR (1.03 ± 0.02) was recorded in fish acclimated at 26°C and fed D2 (57%FM-43%SBM), and this was significantly lower ($P = 0.031$) than the highest value (D3, 23°C). Neither the main experimental factors (i.e. acclimation temperature and diet) nor their interaction had any significant effect on the thermal growth coefficient (TGC) (Table 2).

Preferred temperature

A two-way ANOVA showed that only acclimation temperature had a significant effect ($P = 0.001$) on the preferred temperature; neither diet ($P = 0.99$) nor the interaction ($P = 0.08$) between the two experimental factors had any significant effect on this variable.

The highest preferred temperature (27.7°C) selected by fish acclimated at 23ºC was significantly higher than the lowest temperature (26.4°C) preferred by totoabas acclimated at 26°C (Fig. 1).

Critical thermal maximum (CTMax)

The CTMax was defined as the temperature at which 100% of the fish evaluated showed the loss of equilibrium response. A two-way ANOVA showed that both temperature ($P = 0.001$) and diet ($P = 0.047$) had a significant effect on CTMax, but there was no significant interaction effect ($P = 0.087$). Fish resistance decreased as the percentage of SBM in the diet increased (Fig. 2).

Table 2. Biological performance (average ± standard deviation) of juvenile *Totoaba macdonaldi* acclimated at 23 or 26°C and fed four diets containing different replacement levels of fish meal with soybean meal. Two-way ANOVA (n = 24) was used to evaluate the effect of acclimation temperature, experimental diets, and the interaction between these two factors. Dunnett's *post-hoc* test was used to compare the fish meal replacement treatments versus the control diet (CD). Fisher's least significant difference test was used to test for differences between the experimental treatments' means. All analyses were performed at a 0.05 significance level. Letters (a, b) denote significant differences between CD and treatments. Letters (w, x, y) denote significant differences between treatments. CD: 100%FM. Diet 1 (D1): 68%FM-32%SBM. Diet 2 (D2): 57%FM-43%SBM. Diet 3 (D3): 44%FM-56%SBM. SBM: soybean meal, FM: fish meal, SGR: specific growth rate, FCR: feed conversion ratio. TGC: thermal growth coefficient.

Biological indices	Temperature								*P*
	23°C				26°C				
	CD	D1	D2	D3	CD	D1	D2	D3	
Survival (%)	100.0 ± 0.0	97.0 ± 5.20	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	100.0 ± 0.0	>0.05
Initial weight (g)	100.4 ± 2.0	104.4 ± 2.0	107.7 ± 2.0	106.0 ± 0.4	105.0 ± 3.0	104.6 ± 0.3	104.2 ± 1.4	101.7 ± 0.5	>0.05
Final weight (g)	240.6 ± 5.0	230.3 ± 14.0^{y}	223.0 ± 9.0^{y}	235.0 ± 25.0^{xy}	249.4 ± 12.0	258.0 ± 9.2^{wx}	264.2 ± 7.9^{w}	259.7 ± 25.0^{wx}	<0.05
Weight gain (%)	139.6 ± 9.0	120.7 ± 15.0^{xy}	107.2 ± 12.2^{y}	121.6 ± 23.7^{xy}	137.8 ± 16.6	146.7 ± 8.8^{wx}	153.6 ± 10.0^{w}	155.9 ± 30.3^{w}	<0.05
SGR (% d^{-1})	1.37 ± 0.04	1.31 ± 0.11^{xy}	1.25 ± 0.06^{y}	1.33 ± 0.17^{xy}	1.44 ± 0.02	1.49 ± 0.06^{wx}	1.53 ± 0.05^{w}	1.49 ± 0.16^{w}	<0.05
FCR	0.99 ± 0.02^{a}	1.07 ± 0.04^{abwx}	1.10 ± 0.05^{abwx}	1.13 ± 0.09^{bx}	1.03 ± 0.03^{ab}	1.04 ± 0.03^{abw}	1.03 ± 0.02^{abw}	1.10 ± 0.07^{abwx}	<0.05
TGC	1.12 ± 0.05	1.01 ± 0.10	0.93 ± 0.08	1.02 ± 0.16	0.99 ± 0.09	1.04 ± 0.051	1.08 ± 0.05	1.08 ± 0.15	>0.05

There were significant differences in the CTMax of fish fed CD *vs*. fish fed SBM diets. The CTMax (37.3°C) of fish acclimated at 23°C and fed CD was significantly lower ($P < 0.0001$) than the CTMax (38.2°C) of fish fed the same diet but acclimated at 26°C. The CTMax observed in this treatment (CD, 26°C) was also significantly different versus most other treatments, except for fish fed D1 and acclimated at 26°C (37.8°C; $P = 0.12$).

The highest average CTMax (37.8°C) was recorded in fish acclimated at 26°C and fed D1 (68%FM-32%SBM); this was significantly higher relative to fish acclimated at 23°C and fed D2 (37.3°C; $P = 0.01$) or D3 (37.2°C; $P = 0.003$). The lowest CTMax was observed in totoabas acclimated at 23°C and fed D3; this was significantly lower relative to fish acclimated at 26°C and fed D1 ($P = 0.003$), D2 (37.6°C; $P = 0.02$), or D3 (37.7°C; $P = 0.014$) (Fig. 2).

DISCUSSION

Biological performance

This study evaluated the interaction effect of temperature and the quality of diets formulated by replacing FM with SBM in varying proportions (32, 43, and 56%) on the performance of *Totoaba macdonaldi*. Survival after 61 days of cultivation was unaffected by either acclimation temperature or percent SBM in the diet. Fish acclimated at 23 and 26°C, recorded 100% survival; a 97% survival was recorded in the 23ºC × D1 treatment because one fish jumped out of the tank. Similar high survival rates (>97%) have been reported for *T. macdonaldi* acclimated at 23°C and fed diets in which FM was replaced either with 15 to 100% soy protein concentrate (SPC), supplemented or not with 1% taurine (Bañuelos-Vargas et al. 2014, López et al. 2015, Trejo-Escamilla et al. 2016), or with 24, 44, or 64% SBM with 1% taurine (Fuentes-Quesada et al. 2018). High survival rates have been reported for other species in the family Sciaenidae such as *Nibea miichthioides* (Wang et al. 2006), *Argyrosomus regius* (Velazco-Vargas et al. 2013), *Sciaenops ocellatus*, and *Cynoscion parvipinnis* (Minjarez-Osorio et al. 2016) when fed diets containing varying percentages of SBM (15 to 100%) or SCP (25 to 75%). However, those authors did not evaluate the interaction effect between temperature and diet quality. Our study highlights the importance of this interaction to know the performance of *T. macdonaldi* because, in culture conditions, the thermal variation has a marked influence on fishes' physiology.

Average weight, specific growth rate, and percentage weight gain were all influenced only by acclima-

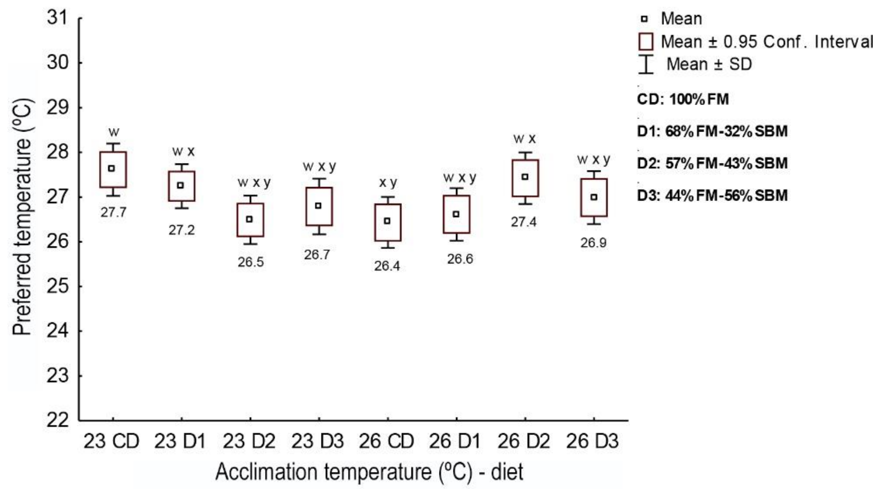

Figure 1. Preferred temperature (average ± standard deviation, SD) of juvenile *Totoaba macdonaldi* acclimated at 23 and 26°C and fed four diets containing different levels of replacement of fish meal (FM) with soybean meal (SBM). Two-way ANOVA (n = 24 per treatment) were used to evaluate the effect of acclimation temperature, experimental diets, and the interaction between these two factors. Dunnett's *post hoc* test was used to compare the fish meal replacement treatments *vs*. control diet (CD). Fisher's least significant difference test was used to test for differences between the experimental treatments' means. All analyses were performed at a 0.05 significance level. Letters (w, x, y) denote significant differences between treatments.

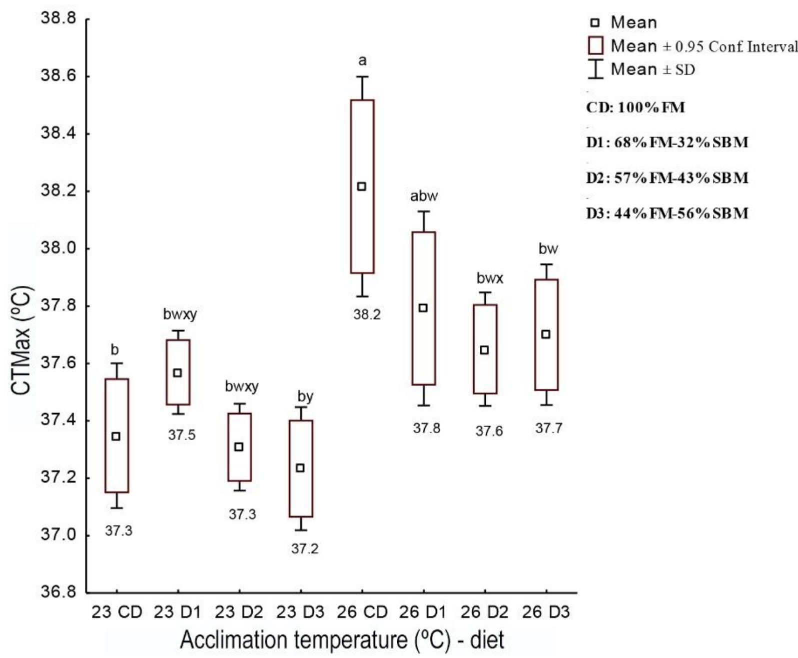

Figure 2. Critical thermal maximum (average ± standard deviation, SD) of juvenile *Totoaba macdonaldi* acclimated at 23 and 26°C and fed four diets containing different levels of replacement of fish meal (FM) with soybean meal (SBM). Two-way ANOVA (n = 96) were used to evaluate the effect of acclimation temperature, experimental diets, and the interaction between these two factors. Dunnett's *post-hoc* test was used to compare the fish meal replacement treatments *vs*. control diet (CD). Fisher's least significant difference test was used to test for differences between the experimental treatments' means. All analyses were performed at a 0.05 significance level. Letters (a, b) denote significant differences between CD and treatments. Letters (w, x, y) denote significant differences between treatments. CTMax (°C): critical thermal maximum.

tion temperature. The highest values for these indices were observed in fish acclimated at 26°C. The lowest weights were recorded in fish acclimated at 23°C and fed diets containing varying percentages (32, 43, and

56%) of soybean meal. In our study, the higher values were obtained in the percent weight gain (WG) and SGR, compared to those reported for this same species by Espinosa-Chaurand et al. (2015), Perez-Velazquez et al. (2016), and González-Félix et al. (2018) (Table 3).

The differences in SGR values between our study and works by other authors could be related to initial fish weight, the diets tested (with zero or low percent SBM), and the thermal conditions under which those studies were conducted. Our results for average weight, specific growth rate, and percent WG in juvenile *T. macdonaldi* might be due to the thermal condition at which fish were acclimated, being 26°C similar to their preferred temperature (26.3°C; Talamás 2001). This temperature could be the optimal condition for totoaba so that their biochemical and metabolic processes are most efficient (Beitinger & Fitzpatrick 1979), suggesting that fish make better use of the energy obtained from the diet and allocate it to improved performance and growth (Brett 1956, Schram et al. 2013).

Food is a major economic factor in aquaculture, so it is important to use and efficiently provide adequate diets for cultured species (Lekang 2015). FCR is an index that reflects the conversion of food consumed relative to body weight gained (Tacon 1987) and is commonly used to assess economic viability (NRC 2011a). The FCR of *T. macdonaldi* was influenced only by the experimental diets. The lowest FCR (0.99 ± 0.02) was attained by fish fed the diet with no SBM, and the highest (1.13 ± 0.09) with the 56% SBM diet. The FCR range observed in our study was similar to the one reported by Fuentes-Quesada et al. (2018) for this same species (0.82 ± 0.03 to 1.11 ± 0.07) but lower than the one recorded by Madrid et al. (2019) (1.11 ± 0.09 to 1.34 ± 0.03). In our study, the FCR of fish acclimated at 23°C showed a tendency to increase as the proportion of FM replacement increased. The increase in FCR might be because replacing a higher proportion of FM (43 and 56%) reduces food digestibility due to the high carbohydrates level, particularly non-starch polysaccharides (NSP). Fish fed low-digestibility diets require more food to achieve the same weight gain, resulting in a high FCR (NRC 2011a).

The thermal growth coefficient (TGC) index predicts fish weight relative to water temperature (Alanärä et al. 2001). The *T. macdonaldi* TGC was not influenced by either acclimation temperature or diet and ranged between 0.93 ± 0.08 (D2 at 23°C) and 1.12 ± 0.05 (CD at 23°C). These indexes are higher than those reported by Perez-Velazquez et al. (2016) (0.018 ± 0.009 to 0.071 ± 0.024) when they evaluated the level of lipids in the diet of juveniles of this species acclimated at 28.3°C. Our values are also higher than those reported by González-Félix et al. (2018) when evaluating diets with prebiotic supplements and commercial probiotics in juveniles (215.6 ± 9 g) acclimated at 27.67°C (Table 3). TGC values within the range observed in our study were reported by Mata-Sotres et al. (2018) for juvenile *T. macdonaldi* (9.5 ± 0.1 g) when they evaluated the effect of adding DHA to diets based on chicken-waste meal using tallow instead of fish oil to meet the lipid requirements.

TGC values ranged between 0.7 and 1.1 (± 0.2) in juveniles totoaba (2.7 ± 0.1 g) acclimated at 26.0°C and fed diets containing chicken waste meal as an alternative protein source, as determined by Badillo-Zapata et al. (2016). These values are closer to those obtained in our study (Table 3), probably because both studies used an alternative protein source that influenced the fish nutritional status, and an acclimation temperature similar to the one preferred by this species.

Fuentes-Quesada et al. (2018) recently documented that the increase of SBM as the protein source in the diet affected the TGC of juvenile *T. macdonaldi* acclimated at 23.3 ± 1.1°C (Table 3). They reported TGC values ranging between 1.21 and 1.61, and this index increased as the proportion of SBM decreased (22%). In our study, neither acclimation temperature nor diet influenced the TGC (0.93 to 1.12) of juvenile *T. macdonaldi*; the values are low and differ in 0.28 to 0.49. Other studies have reported that TGC may be negatively affected (Cho & Bureau 1998) when fish are grown in unfavorable environmental conditions (Kaushik 1998) or fed diets that do not meet their nutritional requirements. In those conditions, fish use a larger amount of energy to perform biological functions such as survival and growth (Willmer et al. 2005, Crawshaw & Podrabsky 2011).

Also, TGC can increase at low temperatures and decrease at high thermal values (Koskela et al. 1997). In our study, the TGC of totoaba acclimated at 26°C was higher and increased in 0.04 and 0.09 units (relative to the control) when SBM was included in diets D1 and D2. Based on the TGC values reported for this species, we suggest that a range between 0.7 and 1.1 is acceptable for this index if the thermal preference interval or the final preferendum (26.3°C) of juvenile *T. macdonaldi* is considered since some physiological processes are more efficient under such thermal conditions.

Preferred temperature

The preferred temperature has been studied in several marine fish species, including *Clupea pallasi*, *Sardinops melanostictus*, *Oncorhynchus keta*, *Pagrus major*, *Oplegnathus fasciatus*, *Trachurus japonicus*,

Table 3. Biological indices of juvenile *Totoaba macdonaldi* fed different replacement levels of fish meal with soybean meal (SPC: soy protein concentrate or SBM: soybean meal) or without soy in the diet at different temperatures. SGR: specific growth rate, TGC: thermal growth coefficient.

Author	Temperature (°C)	Replacement proportion with SBM (%)	Initial weight (g)	Survival (%)	Final weight (g)	Weeks	SGR (%)	TGC
Rueda-López et al. (2011)	25.0	without soy	12.1 ± 0.09	82.2-100	30.0 ± 1.9 to 84.0 ± 2.7	10	1.2 ± 0.1 to 2.2 ± 0.0	---
Minjarez-Osorio et al. (2012)	28.4	without soy	74.7 ± 5	93-100	197.0 ± 2 to 203.6 ± 2	8	1.7 ± 0.2 to 1.8 ± 0.2	---
Bañuelos-Vargas et al. (2014)	23.0	30 SPC 60 SPC	7.5	99	not reported	6	---	---
López et al. (2015)	23.5	30 SPC 60 SPC	7.5 ± 0.5	97.9-100	not reported	8	---	---
Espinosa-Chaurand et al. (2015)	20.5	---	26.3 ± 4.7	88.8-100	30.81 ± 2.9 to 46.0 ± 1.7	8	0.26 ± 0.14 to 0.99 ± 0.06	---
Badillo-Zapata et al. (2016)	26.0	without soy	2.7 ± 0.1	52.4-89.3	20.7 ± 3.4 to 53.2 ± 1.8	12.2	---	0.7 - 1.1
Pérez-Velázquez et al. (2016)	28.3	without soy	128.3 ± 9.9	95-100	148.25 ± 16.79 to 227.59 ± 36.64	8	0.30 ± 0.15 to 1.09 ± 0.35	0.018 - 0.071
Trejo-Escamilla et al. (2016)	23.0	15 to 100 SPC	50.0 ± 1.0	97-100	103.9 ± 1.8 to 143.9 ± 28	8.5	---	---
Barreto-Curiel et al. (2018)	26.0	---	3.0 ± 0.2	94.3-97.1	22.7 ± 0.3 to 28.1 ± 0.3	8.6	3.4 ± 0.0 to 3.7 ± 0.0	---
Fuentes-Quesada et al. (2018)	23.3	22, 44 and 64 SCP+SBM	71.7 ± 35.7	not reported	not reported	8	---	1.21 - 1.61
González-Félix et al. (2018)	27.67	21.81	215.6 ± 9.3	97.5-98.3	387.2 ± 30.9 to 399.1 ± 38.8	15.6	0.54 ± 0.05 to 0.56 ± 0.9	0.04 - 0.05
Mata-Sotres et al. (2018)	26.0	without soy	9.5 ± 0.1	92.4-100	45.9 ± 1.4 to 47.9 ± 2.2	9	2.58 ± 0.05 to 2.64 ± 0.04	0.90 - 0.93
This study	23.0-26.0	32, 43, 56	100.4 ± 2.0 to 107.7 ± 2.0	97.0-100	223.0 ± 9.0 to 264.2 ± 7.9	11	1.19 ± 0.10 to 1.53 ± 0.05	0.93 - 1.12

and *Pseudocaranx dentex* (Tsuchida 1995); *Gadus morhua* (Lafrance et al. 2005), and *Paralichthys californicus* (Esquer-Méndez et al. 2010), to determine the thermal range chosen by fish or predict the optimum temperature for growth, e.g. *Polyprion oxygeneios* (Khan et al. 2014) and *Solea solea* (Schram et al. 2013). Only one study aimed to determine the preferred temperature of *T. macdonaldi* (Talamás 2001) has been conducted to date. The final preferred temperatures for 2- and 3-month old juveniles were 26.3 and 25.2°C, respectively. The studies referred to above and the one by Talamás (2001, *unpubl. data*) examined only the effect of temperature but not the effect of diet quality.

Some studies have evaluated the effect of both temperature and diet. However, these have focused on fish's biological performance, including growth in weight, e.g. in hapuku *Polyprion oxygeneios* (Tromp et al. 2016) or the body chemical composition and incidence deformities in juvenile tench, *Tinca tinca* (Kamiński et al. 2017).

Our study evaluated the interaction effect of temperature and diet quality on the preferred temperature and thermal resistance of totoaba. Our results demonstrated that the preferred temperature of juvenile *T. macdonaldi* was influenced only by acclimation temperature. This response could be attributed to several aspects, including the recent thermal history of the fish (acclimation temperatures), which strongly influences the thermal range selected (Fry 1947), and the thermal history characteristic of the species (Kelsch & Neill 1990) since juveniles are commonly found between 25 and 29°C in surface waters in their natural environment (Flanagan & Hendrickson 1976).

In this study, juvenile *T. macdonaldi* preferred temperatures higher than their acclimation temperature, which was more evident in fish conditioned at 23°C. This behavior may suggest a possible adaptive relationship between acclimation temperature and preferred temperature, in which fish chose new thermal values that would maximize various physiological functions, at least at a level higher than the one previously reached at the acclimation temperature (Kelsch & Neill 1990).

Regarding the diet, it has been reported that replacing up to 60% of FM with soy protein concentrate (SPC) does not affect the yield of *T. macdonaldi* (Bañuelos-Vargas et al. 2014, López et al. 2015, Trejo-

Escamilla et al. 2016). In this study, diets with different percentages of soybean (32, 43, and 56%) seemed to meet the nutritional requirements of the biological performance of *T. macdonaldi* and did not affect its preferred temperature. All the fish exposed to the thermal interval during the preferred temperature tests were active along the channel and did not experience thermal stress, which would have caused a higher energy expenditure to avoid adverse conditions.

Critical thermal maximum: CTMax

Fish physiological condition is key when performing tolerance and thermal resistance tests (Paladino et al. 1980) using either static or dynamic methods (Fry 1947, Beitinger & Bennett 2000, Beitinger et al. 2000). The CTMax test is used to determine temperature resistance since it evaluates the fish's requirements at the thermal, physiological, and ecological levels (Lutterschmidt & Hutchison 1997). When CTMax is evaluated in fish, the general tendency is for this indicator to increase with acclimation temperature (Paladino et al. 1980), as observed in species such as *Sardinops sagax* (Martínez-Porchas & Hernández-Rodríguez 2010), *Acipenser brevirostrum* (Zhang & Kieffer 2014), and *Pseudocrenilabrus multicolor* (McDonnell & Chapman 2015).

Several different behavioral responses were observed in juvenile *T. macdonaldi* when exposed to increased water temperature to evaluate their resistance. First, they showed increased activity, followed by muscle spasms (MS) and finally losing equilibrium (LE). These responses have been observed in many species, including blenny fish C*orypho-blennius galerita*, old fish *Gobius paganellus*, goby *Lipophrys pholis*, futarra fish *Paralipophrys trigloides* (Vinagre et al. 2013), and *Pseudocrenilabrus multicolor* (McDonnell & Chapman 2015); they are part of organisms' natural behavior to avoid thermal conditions that are adverse for their vital functions (Cowles & Bogert 1944, Paladino et al. 1980). The MS and LE responses are considered excellent indicators of thermal behavior in fish, as they characterize the endpoint to evaluate CTMax when observed in 100% of the organisms (Lutterschmidt & Hutchison 1997).

In this study, when the LE response was observed in 100% of the fish evaluated, it was considered the endpoint to determine the CTMax of juvenile *T. macdonaldi*; it was influenced by both acclimation temperature and diet. The lowest temperature for LE was observed in fish acclimated at 23°C and fed the highest proportion of SBM (56%: D3). The highest temperature for LE response was observed in fish acclimated at 26°C and fed CD (100% FM).

Unlike our study, other studies on the thermal resistance of fish have not considered the effect of diet quality, mostly when plant-based meals replace the fish meal. Our results with *T. macdonaldi* show the implications that including a high proportion of SBM in the diet might have on CTMax, which is used as an indicator of adaptation and stress in fish (Paladino et al. 1980).

The highest CTMax was recorded in fish acclimated at 26°C and fed the control diet (i.e. no SBM). On the other hand, the lowest CTMax was observed in fish acclimated at 23°C and fed the diet containing the highest proportion of SBM (56%: D3). Although this diet (D3) had no significant effect on survival and other biological performance variables, it significantly affected thermal resistance. It is likely that diets containing a high SBM level (43 and 56%) also had a high content of non-starch polysaccharides (NSP). High NSP levels in fish diets might have adverse effects due to their ability to bind organic and inorganic molecules, which may hinder the use of other nutrients (NRC 2011a). Also, NSPs are a low energy source for fish and affect the digestibility of lipids (NRC 2011a), which could restrict energy production. These considerations possibly influenced the energetic capacity of fish (Jobling 1997); however, complementary studies on other aspects of the energy physiology of totoaba are necessary to understand better the effect of diets where FM has been partially replaced by SBM on the thermal resistance of this species.

Our results showed that, except for thermal resistance, feeding juvenile *T. macdonaldi* with diets containing a high percentage of SBM did not affect their survival, growth in weight, or preferred temperature when acclimated at 26°C - similar to their thermal optimum. Further studies on the interaction effect of temperature and the inclusion of vegetable (soybean) meal as a fishmeal replacement in the diet, and its potential effect on CTMax, are needed to use this indicator to predict the response capacity of *T. macdonaldi* under different thermal conditions. Our study laid the basis for considering other biological indicators to determine the feasibility of using SBM in the diet of juvenile *T. macdonaldi.*

ACKNOWLEDGMENTS

The Federal Government of Mexico supported this study through the regular funding of CICESE, project number: 623151, and for bonding project with State Commission of Public Services of Tecate (CESPTE, for its acronym in Spanish) number 9269. Thanks especially to Centro Reproductor de Especies Marinas del Estado de Sonora (CREMES), at Bahía Kino, Sonora, Mexico, for providing the totoaba eggs, and the Instituto de Investigaciones Oceanológicas de la Universidad Autónoma de Baja California (IIO-UABC) for allowing the use of recirculation systems and preparation of experimental diets. We are also grateful to Dr. Fernando Barreto Curiel for his support in preparing the diets and Luis Murillo Valenzuela, Jesús Mariscal Medina, and Adrian Celaya Ortega's technical assistance. María Elena Sánchez-Salazar edited the English manuscript.

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Received: 14 May 2020; Accepted: 8 November 2020

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