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Research Article

Influence of temperature on respiratory metabolism during early development of *Totoaba macdonaldi*

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ABSTRACT. Environmental temperature can act as a positive or negative modulator of the physiology and metabolism of poikilothermic organisms. As a general rule, larvae and juveniles are more sensitive to temperature stress than adults, which represents a key factor that partly determines their development and growth in aquaculture. Therefore, this study analyzed the effect of exposure to temperatures of 21, 24, and 27°C on the respiratory metabolism (RM) of *Totoaba macdonaldi* in different developmental stages. For this purpose, eggs, larvae with 4, 6, 8, 14, and 22 days post-hatch (dph), and juveniles of 25 dph were exposed to the experimental temperatures for 5 h. After the exposure time, oxygen consumption measurements were performed. The results clearly show that temperature (21 to 27°C) has the greatest effect on RM in eggs and larvae at 4 and 22 dph (3.1 ± 0.3 to 4.3 ± 0.3 µmol O_2 h^{-1} egg^{-1}, 2.9 ± 0.3 to 10.5 ± 1.2 µmol O_2 h^{-1} $larvae^{-1}$ and 102.0 ± 6.4 to 189.8 ± 15.3 µmol O_2 h^{-1} $larvae^{-1}$, respectively). This thermal sensitivity was not observed from 6, 8, and 14 dph larvae and juveniles at 25 dph, where morphological development was the main factor that influencing the RM. Therefore, this study shows that temperature affects RM in different development stages of totoaba, beginning in the egg stage and intensifying once the larvae hatch until 22 dph. Understanding how temperature affects energy expenditure by measuring RM is essential to establish culture conditions that allow better physiological performance and growth in the early life stages of *T. macdonaldi*.

Keywords: *Totoaba macdonaldi*; acute thermal exposure; respiratory metabolism; early development; aquaculture

INTRODUCTION

Temperature is a key driver of physiological, metabolic, and behavioral responses in most poikilothermic organisms (Fry 1947, Beitinger & Fitzpatrick 1979). For example, temperature affects fish growth, metabolic rates, development, and reproduction, making them vulnerable to suboptimal thermal conditions (Jobling 1981a,b, Johnston & Dunn 1987, Neubauer & Andersen 2019, Stavrakidis-Zachou et al. 2021). According to Pigliucci et al. (2006), the energy balance of the organism can be related to the thermal sensitivity

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of a species during certain developmental stages. For example, fish can respond to a thermal change in early life stages through phenotypic plasticity, however, if the intensity of the thermal change increases, it could generate different compensatory responses (acclimation) or, in the worst-case scenario, a pessimum or lethal state (Sokolova 2013). In this case, survival depends on maintaining an adequate energetic performance under sub-optimal temperatures (Komoroske et al. 2014).

The physiological performance of most aquatic ectotherms is related to their energy production capacity. As in many other organisms, fish's physiological performance depends on cellular respiration to produce chemical energy (adenosine triphosphate, ATP), which is well represented through the aerobic scope (Schulte 2015). In this case, the energy supply generated by aerobic metabolic pathways is directed to physiological processes, such as maintenance, activity, growth, and reproduction. On the one hand, if an abnormal thermal event occurs, this energy demand can be redirected to express responses that allow escaping from this suboptimal thermal environment or maintaining only the physiological and metabolic processes to preserve life (Sokolova 2013). For this reason, temperature is an especially important factor during the early development stages of fish farmed through aquaculture.

Aquaculture practices often control the temperature during the fish's early life stages to promote optimal growth. If the optimal temperatures are not known, it is possible to relate respiratory metabolism (RM) to the energy demand of fish exposed to different temperatures due to the correlation between growth, respiratory rate, and temperature itself (Laurel et al. 2018, Moyano et al. 2018, Qiang et al. 2019, Prakoso et al. 2019). Identifying the RM thresholds induced by temperatures is crucial to avoid excessive or insufficient energy expenditure at sub-optimal temperatures, and thus, energy requirements can be determined to establish the best nutritional and growing conditions that generate better physiological performance.

Totoaba macdonaldi (Gilbert, 1890) is an endemic fish of the Gulf of California (also known as the Sea of Cortés) classified as critically endangered NOM-059-SEMARNAT-2001 (CITES 2016). For this reason, different institutions have dedicated themselves to studying and cultivating this species to repopulate natural communities and develop sustainable aquaculture (Juárez et al. 2016). At the Universidad Autónoma de Baja California (UABC) in Ensenada, Mexico, totoaba broodstock is kept in recirculating seawater systems where the temperature can range throughout the year from 23 to 25°C (summer) and 18 to 23°C (winter). Juveniles up to 25 ± 2 g are reared in 10,000 L tanks under the same thermal conditions. Later, in the juvenile stage, the organisms are transported to the Gulf of California, where temperatures (24 to 32°C) allow them to grow better (True 2012).

Egg fertilization, hatching, and larval growth of *T. macdonaldi* begin with strict physicochemical water parameters, such as temperature (24°C), dissolved oxygen (>6 mg L^{-1}), and salinity (34). Recirculation systems are also used to care for larvae where strict water management, filtration, and disinfection are implemented. The early development process lasts approximately four or five days post-hatch (dph) when the totoaba opens its mouth and anus (larva 4.1 mm in size). Its morphological development is complete around 28 to 50 dph when the organism acquires the structure of an adult (Peñaz 2001, Galaviz et al. 2015). Undergoing these morphological changes in non-optimal thermal conditions could generate stress associated with high energy requirements, reversible biochemical changes, and acclimation in cultured organisms. Therefore, this study aims to investigate the respiratory metabolism of *T. macdonaldi* at different days of early development (4, 6, 8, 14, and 22 dph) under different temperatures (21, 24, and 27°C). Understanding how temperature affects energy expenditure by measuring RM is essential to establish culture conditions that allow better physiological performance and growth in fish's early life stages, such as *T. macdonaldi*.

MATERIAL AND METHODS

Fish egg and larval rearing

Fish used in this study were obtained from the marine fish hatchery of the Faculty of Marine Sciences at UABC (Universidad Autónoma de Baja California), Ensenada, México. Spawning induction and larval management were performed as reported by True (2012) and Galaviz et al. (2015). After spawning, fertilized (floating) eggs were collected and treated with 100 ppm formalin for 1 h. Later, eggs were rinsed and placed in 2000 L conical bottom tanks with 24°C seawater at a density of 100 eggs L^{-1}. The tanks were connected to a water recirculation system at a rate of 1.5 to 2 L min^{-1} through a fluidized bed biofilter, ultraviolet (UV) sterilizer, and foam fractionator. Eggs hatched approximately 20 h after incubation.

Yolk sac larvae were transferred to 12 100-L rearing tanks at a density of 100 ind L^1 and cultured under the same growing conditions as in the hatching process (24ºC, salinity of 34, 6 mg O_2 L^{-1}). According to Galaviz et al. (2015), larval feeding was performed at 3 to 4 dph; thrice a day (08:00, 12:00 and 18:00 h). Feeding consisted of live prey, starting with enriched rotifers (*Brachionus plicatillis*) with fatty acids (Bio-Marine Algamac 3050™, CA, USA) at 5 rotifers mL^{-1} for the first three days. At 10 dph, the diet was followed by *Artemia* nauplii (Salt Creek Inc, Salt Lake City, UT, USA) at a concentration of 0.6 nauplii mL^{-1}. *Artemia* metanauplii were used at a concentration of 5 metanauplii mL^{-1} from 12-16 dph. At 27 to 30 dph, the amount of live feed was reduced, and a combination of enriched *Artemia* metanauplii and micro-diet (Otohime, Japanese marine weaning diet, red mari-culture; protein 52.1%, lipids 16.3%, ash 11.2%, particle size 200-1410 µm) was used. This research was performed at UABC with standard procedures (Permit N°DGVS-CR-IN-1084-BC/09SEMARNAT) and complied with the Guidelines of the European Union Council (2010/63/EU) and the Mexican Government (NOM-062-ZOO-1999) for the production, care and use of experimental animals.

Oxygen consumption measurement

Oxygen consumption of the organisms exposed to temperatures of 21, 24, and 27°C was measured to assess the effect of temperature on their respiratory metabolism (RM) at different early development stages (egg, larvae at 4, 6, 8, 14, and 22 dph, and juveniles of 25 dph). For this purpose, the oxygen consumption measurements were performed on organisms exposed for 5 h at each temperature. A closed respirometry system was used, composed of three acrylic plates, each with 24 wells/chambers of 750 µL capacity. Each respirometric plate was placed on an oxygen reader (Sensor Dish Reader®, PreSens, Regensburg, Germany) with an accuracy of ±1% O_2.

The water of two random tanks (24°C) was increased or decreased by 1°C min^{-1} until temperatures of 21 and 27°C were reached. After 5 h of thermal exposure (6 h post spawning), 10 eggs per temperature were transferred to 10 wells with oxygen-saturated seawater at each temperature. This procedure was repeated for each stage of early development (n = 10, 10, 10, 10, 5, 1, respectively). For each totoaba life stage, six chambers without individuals served as controls to account for back-ground respiration (microbial respiration). Dissolved oxygen measurement started immediately after all chambers were hermetically sealed with a silicone membrane and placed in thermoregulated baths. Oxygen concentration was recorded every 5 min for 1 h and ended when dissolved oxygen in the chambers decreased by more than 30% of saturation to avoid any additional stress in the organisms (Díaz et al. 2007, Peck & Moyano 2016).

Data obtained were expressed as µmol O_2 h^{-1} egg^{-1}, $larva^{-1}$, or $juvenile^{-1}$, respectively. The RM was determined from the difference between the initial oxygen value and final dissolved oxygen concentration throughout the incubation. The fish had fasted 24 h before the oxygen consumption measurement (when applicable) to avoid the effects of digestive processes on oxygen consumption rate (Jobling 1981b, Beamish & Trippel 1990, Chabot et al. 2016a,b, Peck & Moyano 2016).

Data were previously tested for normality and homogeneity of variances, and RM data obtained at each condition were analyzed using a separate univariate analysis of variance (ANOVA). All data were expressed as mean ± standard error (SE), and the significance of the main effects was assessed by a *P*-value <0.05. Values were compared using Tukey's post hoc test, taking the *P*-value (<0.05) as the threshold. In addition, covariance analysis was performed for the evaluation of *T. macdonaldi* larvae oxygen consumption rate during their development, using a quadratic model ($y = a + bx^2$) and linearized using the natural logarithm of oxygen consumption (O_2 h^{-1} $larvae^{-1}$) and comparison of the slopes (consumption rates) using the least-squares model.

RESULTS

After obtaining *Totoaba macdonaldi* fertilized eggs, they were exposed to the experimental temperatures (21, 24, and 27°C) to analyze the effect of temperature on respiratory metabolism. The oxygen consumption of *T. macdonaldi* eggs exposed to the three temperatures appeared to increase as temperature increased from 3.1 ± 0.3 to 4.3 ± 0.3 µmol O_2 h^{-1} egg^{-1} ($P > 0.05$; Fig. 1a).

Similarly, oxygen consumption of larvae with four dph was influenced by acclimation temperature (21, 24, and 27°C) increasing significantly from 2.9 ± 0.3, 5.3 ± 0.5, and 10.5 ± 1.2 µmol O_2 h^{-1} $larvae^{-1}$ ($P < 0.05$), respectively.

For larvae with 6 dph, the oxygen consumption rate at 21 and 24°C had a similar value (4.9 ± 0.5 and 5.7 ± 0.5 µmol O_2 h^{-1} $larvae^{-1}$) and decreased significantly at 27°C (3.8 ± 0.4 µmol O_2 h^{-1} $larvae^{-1}$; $P < 0.05$). Oxygen consumption was similar in larvae at 8 dph at all three acclimation temperatures (11.0 ± 0.8, 9.3 ± 0.7, and 10.4 ± 0.8 µmol O_2 h^{-1} $larvae^{-1}$; $P > 0.05$). For larvae at 14 dph, oxygen consumption was 22.9 ± 1.6 µmol O_2

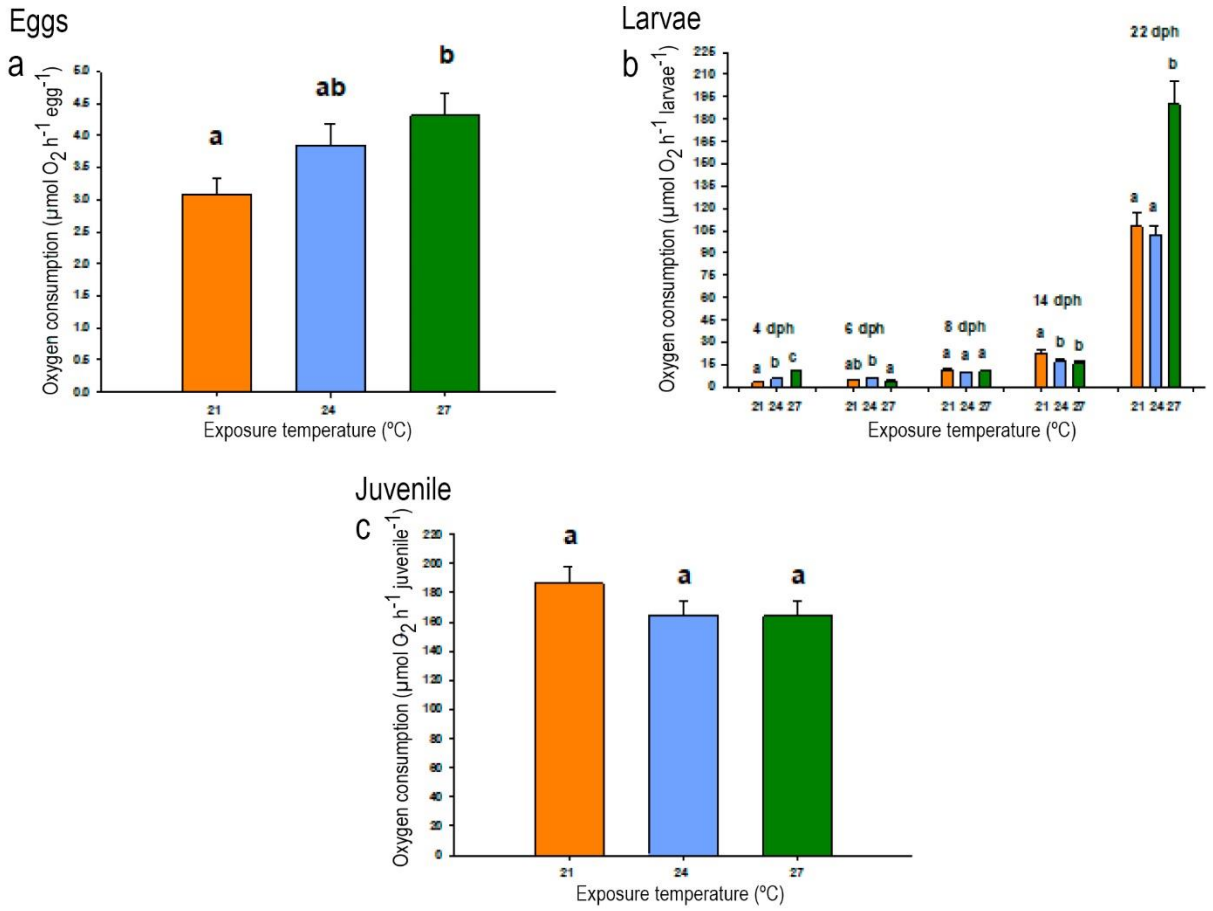

Figure 1. Oxygen consumption of *Totoaba macdonaldi*; a) eggs; b) 4, 6, 8, 14 and 22 days post-hatching (dph); and c) juveniles 25 dph. Oxygen consumption at each early developmental stage was assessed at acclimation temperatures of 21, 24, and 27 °C. Statistical differences ($P < 0.05$) are represented with lowercase letters (a, b, c).

h^{-1} $larvae^{-1}$ ($P < 0.05$) at 21°C and remained at 16.9 ± 1.1 and 15.5 ± 1.3 µmol O_2 h^{-1} $larvae^{-1}$ at 24 and 27°C (Fig. 1b).

Oxygen consumption increased considerably for larvae at 22 dph when it was observed similar from 21-24°C (107.9 ± 9.8 and 102.0 ± 6.4 µmol O_2 h^{-1} $larvae^{-1}$ respectively, $P > 0.05$), increasing significantly ($P < 0.05$) to 189.8 ± 15.3 µmol O_2 h^{-1} $larvae^{-1}$ at 27°C (Fig. 1b). Finally, in juveniles 25 dph oxygen consumption remained similar with a range from 164.0 ± 10.3 to 186.4 ± 11.6 µmol O_2 h^{-1} $juvenile^{-1}$ ($P > 0.05$) (Fig. 1c).

The oxygen consumption rates (O_2 h^{-1} $larvae^{-1}$) during the first 25 dph of *T. macdonaldi* showed high correlation coefficients (0.80-0.88) among the three larval culture temperatures (Fig. 2). The comparison of the oxygen consumption rates (slopes) shows significant differences for larvae cultured at 21 and 27°C compared to those cultured at 24°C ($P < 0.05$).

DISCUSSION

Totoaba macdonaldi is a species of great ecological, social and nutritional importance in northwest Mexico (Juárez et al. 2016). This organism was classified as a critically endangered species because it was fished almost to extinction during the first half of the 20th century (Pedrín-Osuna et al. 2001). For this reason, different projects have been oriented to study and understand their physiological and metabolic requirements. Therefore, this study aims to analyze the effect of different culture temperatures on respiratory metabolism as an indicator of energy requirements at each temperature. This information may expand the necessary knowledge to improve totoaba rearing in the early life stages.

High or low metabolic rate has been commonly observed in poikilotherms in response to energy demand

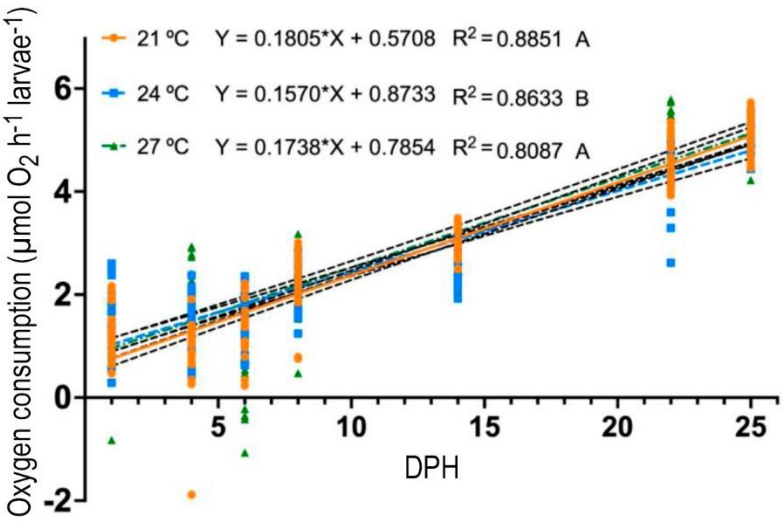

Figure 2. Oxygen consumption rates (µmol O_2 h^{-1} $larvae^{-1}$) of *Totoaba macdonaldi* larvae during the first 25 days post-hatching (DPH). The capital letters at the end of each equation represent the significant differences ($P < 0.05$) between natural logarithm of oxygen consumption slopes curves and temperature treatments after the covariance analysis.

with changes in temperature (Schulte 2015), where a common response could be observed; 1) a lower rate of oxygen consumption at low temperatures due to a decrease in cellular kinetics and slower metabolic reactions (generally accompanied by lower feed efficiency and reduced growth); and 2) a significant increase in the respiratory rate at high temperatures, interpreted as a response to produce more energy through aerobic metabolism and growth (Sokolova 2013, Prakoso et al. 2019). After exposing the organisms to temperatures of 21, 24, and 27°C for 5 h, we could observe that the eggs (6 h post spawning) and larvae at 4 and 22 dph tended to increase their oxygen consumption concerning temperature increase. This increase in oxygen consumption rate due to thermal increase has been observed in different larvae and juveniles, such as the Atlantic herring (*Clupea harengus*) at 18 to 32 dph in cold temperatures (5°C) compared to higher temperatures (15°C); rainbow trout (*Oncorhynchus mykiss*) embryonic development at 5, 10, 15 and 17.5°C; and yellowtail amberjack (*Seriola lalandi*) juveniles acclimated at 20 to 32°C, among other larval and juvenile fish (Peck & Buckley 2008, Peck & Moyano 2016, Moyano et al. 2018, Larios-Soriano et al. 2021, Melendez & Muller 2021). As mentioned above, the increase in oxygen consumption rate concerning temperature has been widely described as an energetic response to generate high energy levels (Sokolova 2013). In these cases, energy production is used to recover energetic homeostasis under sub-optimal conditions or exhibit high food consumption and growth rates at optimal conditions (Prakoso et al. 2019).

Establishing a relationship between respiratory and metabolic rates and the body size of larvae is difficult because the metabolic rate scales allometrically with body size (Giguère et al. 1988, Moyano et al. 2018). However, evidence has shown that an increase in metabolic rate is required for fast-growing larvae. Bang et al. 2007 determined through the structure of the *Clupea harengus* otoliths that a high standard metabolic rate is a prerequisite for rapid growth along with other factors, such as maternal effects, genetics, and previous larval growth history. However, a high standard metabolic rate (high energy demand) does not necessarily affect larval survival because of factors such as feeding success.

The high RM in the eggs (6 h after spawning) and larvae of 4 and 22 dph exposed at 27°C could indicate better growing conditions. Increased metabolic rate in marine fish larvae has been widely related to faster growth (Metcalfe et al. 1995, Bang et al. 2007). On the other hand, the temperature is well known to be strongly responsible for the growth of fish larvae, such as striped bass (*Morone saxatilis*) at 25 dph exposed at >12 to <22°C and bay anchovy (*Anchoa mitchilli*) larvae exposed at >25 to <27°C (Secor & Houde 1995, Rilling & Houde 1999 in Houde 2008). However, this effect on larval growth occurs only during periods of high food availability (Bang et al. 2007). In this case, the eggs and even larvae with 4 dph have a yolk sac, so the increased metabolism observed in this study could

lead to more rapid consumption of this energy reserve. Larvae with 22 dph have completed the development of the digestive glands (Galaviz et al. 2015), thus, they are dependent on exogenous food. For these 22 dph larvae exposed to 27°C, the temperature could favor greater activity and food consumption since, according to this study's results, there is greater energy demand. However, the totoaba diet should be correctly balanced to take advantage of this increase in metabolism that could lead to further growth. These results may provide evidence that the increase in respiratory metabolism can be positive for larval development and growth, and the metabolic rates can be a good parameter to estimate the possible effect of temperature on energy performance. On the other hand, the RM of the eggs and larvae at 4 and 22 dph and temperatures from 21 to 24°C indicate that they are low to maintain a high metabolism that exhibits temperature-induced metabolic modulation. A low metabolic rate in larvae represents a lower energy demand and lower growth capacity; however, these larvae (with a low metabolic rate) could survive longer during starvation.

Interestingly, larvae with 6, 8, and 14 dph tend to decrease their respiratory metabolism with exposure to 27°C. In this case, lower respiratory metabolism at 27°C in larvae at 6, 8, and 14 dph can be interpreted as lower energy demand and expenditure, probably caused by a decrease in food consumption by a period of starvation or low displacement capacity (Bang et al. 2007, Moyano et al. 2018). According to Galaviz et al. (2015), from days 4 to 16, a series of morphological changes occur in larvae, such as the morphogenesis of the buccopharyngeal cavity and esophagus, mouth, and rectum are open. At 20 dph, the stomach development is complete. A hypothesis is that the gradual increase in respiratory metabolism from 6 to 14 dph is due to growth. However, it is not until the digestive gland development is complete (22 dph) that temperature can increase the feeding rate activity and, thus, the RM. Regarding changes in RM of larvae at 6, 8, and 14 dph, it is possible to relate the most significant effects to morphological development as previously described in fish larvae (Miyashima et al. 2012).

Finally, the RM of the juveniles (25 dph) does not show significant differences but a slight decrease in the fish exposed to 27°C. It could probably be due to the exponential growth rate previously observed in totoaba at 16 dph (Galaviz et al. 2015) that hid the effect of temperatures on the RM. The morphological development of totoaba larvae is completed from 24 to 50 dph (Galaviz et al. 2015, Giffard-Mena et al. 2020), which could suggest that *T. macdonaldi* juveniles possess a high physiological performance that could induce a high metabolic performance. Once the morphological development is complete, the energy demand increases. Therefore, from 22 dph, it is vital to administer a correct balance of nutrients in the diet and an optimal thermal environment that generates the best growth.

Furthermore, according to Peck & Buckley (2008), the effects of temperature on the standard metabolic rate may be less in juveniles compared to the effect on larvae. This result indicates that in some species, such as the Atlantic cod (*Gadus morhua*) or totoaba, growth in the juvenile stage is accompanied by a greater ability to tolerate a wide range of temperatures than larvae. Nevertheless, further studies should be performed to confirm that the gradual increase in respiratory metabolism is due to growth, where morphological modifications are incorporated to strengthen the results in this study.

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