

Article

Modelling Early Growth of *Totoaba macdonaldi* (Teleostei: Sciaenidae) under Laboratory Conditions

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Abstract: The totoaba (*Totoaba macdonaldi*) is a sciaenid (croaker) fish endemic to the Gulf of California with high commercial importance. Because it was considered at risk of extinction (since 2021 it was reclassified as vulnerable by the IUCN), and aquaculture procedures were developed for restocking and commercial purposes. The present study was conducted with the hypothesis that the early stages of totoaba present depensatory individual growth and an observed variance-at-age modelling approach is the best way to parametrize growth. Ten models were tested including asymptotic, non-asymptotic, exponential-like, and power-like curves including a new one that represents a modification of Schnute's model. The model that best described the growth trajectory of larval and early juveniles of *T. macdonaldi* in a controlled environment is a sigmoid curve with two inflexions, related to changes in the feeding regime.

Keywords: endangered marine fish; depensation growth; multi-model inference; Schnute model

Key Contribution: Researchers and entrepreneurs interested in cultivating totoaba will now have a good idea of how larvae grow and what to expect under the laboratory conditions similar to the ones we report. Our work represents the first modelling exercise for totoaba larval growth using state-of-the-art statistical techniques based on information theory.



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1. Introduction

The totoaba, *Totoaba macdonaldi* [1], is a sciaenid species (Teleostei: Sciaenidae) endemic to the Gulf of California. With a maximum length of 2 m, up to 100 kg total weight, and longevity of 27 y [2], it is the largest fish of its family. Totoaba sustained an important commercial fishery that started in the 1920s primarily to collect the swim bladder o maw. The swim bladder is locally named “buche” by Spanish speaking fishers, albeit the word is not an exact translation of swim bladder. Swimming bladders were dried and exported to China where it was considered a delicacy. Along with the swimming bladder market, a commercial meat trade to the United States also developed and became the primary driver of the legal fishery from the 1940s to the 1970s. The commercial fishery rapidly rose and in 1942 the catch peaked at 2261 metric tons. Fishers caught particularly large amounts of totoabas because annually the fish congregate to spawn in the Colorado River Delta and Upper Gulf of California. Catches declined by over 97% to less than 100 tons per year by

the 1970s. Based on declining recorded catch, the totoaba commercial fishery was banned in 1975. In 1976 the totoaba was recorded as endangered in the Mexican federal list of species of interest [3]. Due to efforts of Mexican government and academic institutions to save the totoaba, in 2021 it was reclassified as vulnerable by the International Union for Conservation of Nature (IUCN) [4].

The full life cycle under laboratory conditions has been completed [5]. The original driver for producing totoaba larvae and juveniles was a restocking program. Since 1994, this program has operated through a hatchery working as Environmental Management Unit for Wildlife Conservation (UMA, Spanish acronym) at the Autonomous University of Baja California in Ensenada and San Felipe (Baja California). In 2014, the Aquaculture Institute of the State of Sonora in Kino Bay initiated the production and restocking of captive-bred totoaba, followed by Earth Ocean Farms, a private company in the year 2016. Procedures for brood stock capture, maturation, spawning, larval rearing and juvenile growth-out are completely controlled [6]. Since the early 1990s, institutions have released altogether over 400 thousand juveniles into the wild as part of the restocking program for totoaba conservation, but further study is needed to understand the impact of these releases. They have also provided totoaba juveniles to farming companies and research institutions.

Determining individual growth patterns (length or weight increase over time) allows to understand and improve juvenile fish performance in laboratory rearing operations. Observed size increments are used to parametrize a growth model usually through numerical techniques using regression, likelihood, or Bayesian methods. Likelihood-type fits generally assume normal or log-normal error distributions with constant variance, which has been questioned [7] because variability of length-at-age is commonly found in fish growth studies. Several fitting approaches using variability-at-age have been proposed both for wild [8] and cultured fishes [9].

In the mariculture of fishes, during post larval and early juvenile stages, size grading is a common practice to reduce effects of the common and significant size disparity among individuals of the same age [10]. This practice optimizes feeding rates and reduces cannibalism occasioned by size differences [11]. The term "growth depensation" is used when size variability-at-age increases with age [12]. The reasons why these differences in individual growth occur are not well known; they can be of genetic origin or result of differences in feeding efficiencies or sex-related differential growth [13,14]. In statistical analysis, increasing variability with increasing size is known as multiplicative error; the variance is large when size is large and vice versa [15]. In growth studies when variability-at-size increases with age, models can be parametrized assuming multiplicative errors. Currently, it is commonplace to fit and parametrize growth models considering variability-at-age rather than constant variance, using the growth depensation approach [12] or the observed variance approach [8,9].

It is now common practice to use several "competing" models to describe observed growth in fishes [16–18]. The best model is then selected using coefficient of determination, sum of squared errors or information theory. Reference [16] introduced the multi-model approach (MMA) using the Akaike Information Criterion (AIC) to select the most parsimonious and information-rich model given observed growth data; this approach is now wide-spread in growth studies of fishes, crustaceans, and mollusks. Reference [19] suggested using alternative statistical criteria in selecting individual growth models in fishes. Reference [20] used AIC and Bayesian Information Criterion (BIC) and found both criteria to yield the same hierarchical order in the set of competing models. The slight differences in AIC and BIC are in the penalizing factor of the number of parameters (see reference [21] for a comprehensive explanation).

Based on the behavior of the observed data, the present modelling study was conducted with the hypothesis that the early stages of laboratory reared totoaba exhibit a depensatory individual growth. The study has the following objectives: (1) show how laboratory-reared larvae of the marine fish *T. macdonaldi* exhibits evidence of growth depensation, (2) analyze the early growth performance of totoaba using a multi-model approach,

and (3) introduce a modification in Schnute model to represent early stages of growth in fishes.

2. Materials and Methods

2.1. Ethical Statements

Our study followed the management and cultivation ethical statutes that are mandatory in the activities of the Center for the Reproduction of Marine Species of the State of Sonora (CREMES, Spanish acronym) on the protection of laboratory animals. The optimal conditions were used for the conservation and good care of fish larvae.

2.2. Obtaining the Stock and Culture Conditions

A total of 130,000 viable eggs of *T. macdonaldi* from a brood stock kept in captivity, were obtained through a donation by CREMES. Induction of maturation was achieved through thermal stimulation and photoperiod simulating the seasonal conditions for their reproduction. Spawning was induced by a hormonal implant of ethylamine acetate hydrated salt [des-Gly10, D-Ala6]-LHRH Fish Physiol Biochem 123 (SIGMA), placed in the post-dorsal fin area.

Fertilized eggs (positively buoyant) were collected and separated from the rest by decantation using plastic tubes with a capacity of 1 L, washed with filtered seawater and placed for incubation in a tank with a capacity of 3000 L, at a density of 65 eggs/L. The eggs were counted using the volumetric method described by reference [22]. The incubation was done at an average temperature of 22 °C while the rest of the rearing was conducted with rising temperatures according to the environmental conditions of the outdoor environment. Salinity remained constant at 36 psu. Feeding was provided according to laboratory protocols and consisted of live feed (microalgae, rotifers, *Artemia nauplii*) during the first 30 days post-hatching (DPH), and formulated feed (micro pellets) from 31 until 40 DPH. Temperature, salinity, and dissolved oxygen were recorded daily with a multiparameter YSI Mod 556 MPS.

2.3. Growth

For the egg stage, observations during the first 24 h after spawning were done at two-hour intervals. 24 h is the hatching time of totoaba eggs [23]. Two samples of at least 10 viable eggs were taken in each bi-hourly sample, fixed in 3% formalin and 90% alcohol for further analysis.

Once the larvae hatched, samplings were spread out every four hours during the first 23 days post-hatching (DPH). From 24 to 27 DPH, sampling was done every six hours, and from DPH 28, every 12 h until 40 DPH. In each sampling, at least 20 live organisms were collected; these were photographed fresh using a Motic NC 40 stereoscope with 6× magnification and an integrated camera. The larvae were fixed in equal parts in solutions of 3% formalin and alcohol at 90% for further analysis. The larval total length (TL) was obtained from electronic measurements in the photographs taken with the specialized software Mi Motic Plus 2.0 ML.

2.4. Database

For the formation of the data pairs (age-size), hatching size was the initial size at day zero of the culture. Considering that the sampling periodicity was not continuous, data were grouped per day. To complement the database and strengthen the analysis of larval totoaba growth during their early stages, an exhaustive search was done for information in the published literature that reported growth, preferably under different environmental conditions. The bibliographic data was obtained through digitization using software available online (WebPlotDigitizer 4.6).

2.5. Modelling

A set of ten models (Table 1) were tested using observed length-at-age data to determine which fitted best to growth data of the early stages of totoaba. The von Bertalanffy growth function (VBGF) is the most commonly used model, whereas the logistic has been considered effective to describe growth in farmed tilapia [24]. Both models display monotonic asymptotic size-at-age; however, fish larvae do not grow asymptotically. Therefore, in the present work, a power function, the Tanaka model [25], the persistence model [26] and the extended power models were considered candidates to describe growth [27]. The last two models behave as an age-dependent power function; the Tanaka model is quasi-sigmoid and does not have asymptotic limits [25]. The model of reference [28] was also considered in the set of candidate growth models. This versatile function includes shape parameters that can yield asymptotic, non-asymptotic and power curves. Four cases of the general Schnute model were considered, including a new version, the exponential of Schnute case 1 (Exp-Schnute):

$$L_t = e^{L_1^b} * e^{\left[(L_2^b - L_1^b) \frac{1 - e^{-a(t - \tau_1)}}{1 - e^{-a(\tau_2 - \tau_1)}} \right]} \quad (1)$$

Hence, the complete set of models includes the most likely forms in the early life stages of fish growth. The equations (except for the new one introduced in this paper) are all well-known and can be found in [8,18,27,29]. Growth was analysed assuming increasing variance-at-length. Models were fitted using the following objective function [12]:

$$-LL(\varnothing_i | data) = \sum_i \left[\frac{\ln(2\pi\sigma_i^2)}{2} + \frac{(l_i - \hat{l}_i^2)^2}{2\sigma_i^2} \right] \quad (2)$$

The observed variance-at-age was estimated as:

$$\sigma = \sqrt{\frac{1}{n} \sum (L_{t_{observed}} - L_{t_{calculated}})^2} \quad (3)$$

For each model, parameter estimates were obtained minimizing the objective function using the Newton algorithm [30].

Table 1. The functions and descriptions for each of the ten models.

Models	Function	Parameter Description
EXP-Schnute 1	$Y(t) = e \left[Y_1^b + (Y_2^b - Y_1^b) \frac{1 - e^{-a(t - \tau_1)}}{1 - e^{-a(\tau_2 - \tau_1)}} \right]^{\frac{1}{b}}$	τ_1 is the youngest age in the data set, τ_2 is the oldest age in the data set
Schnute 1	$Y(t) = \left[Y_1^b + (Y_2^b - Y_1^b) \frac{1 - e^{-a(t - \tau_1)}}{1 - e^{-a(\tau_2 - \tau_1)}} \right]^{\frac{1}{b}}$	a : is the constant of the relative growth rate (units in time)
Schnute 3	$Y(t) = \left[Y_1^b + (Y_2^b - Y_1^b) \frac{t - \tau_1}{\tau_2 - \tau_1} \right]^{\frac{1}{b}}$	b : is the incremental relative rate of relative growth rate (dimensionless)
Schnute 4	$Y(t) = Y_1 e^{\left[\log\left(\frac{Y_2}{Y_1}\right) \frac{t - \tau_1}{\tau_2 - \tau_1} \right]}$	Y_1 is the size at age τ_1
Logistic	$Y(t) = \left[Y_1^{-1} + (Y_2^{-1} - Y_1^{-1}) \frac{1 - e^{-a(t - \tau_1)}}{1 - e^{-a(\tau_2 - \tau_1)}} \right]^{-1}$	Y_2 is the size at age τ_2
Bertalanffy	$Y(t) = \left[Y_1 + (Y_2 - Y_1) \frac{1 - e^{-a(t - \tau_1)}}{1 - e^{-a(\tau_2 - \tau_1)}} \right]$	Parameters a and b can be positive, negative or zero.
Power	$Y(t) = a + x^b$	a : is a proportionality constant and b is the power exponent
Extended power	$Y(t) = a * x^{b \frac{c}{x}}$	a, b, c : are constants determined by X
Persistence	$Y(t) = a * x^{b * e(\frac{-c}{x})}$	a, b, c : are constants determined by X
Tanaka	$Y(t) = \left(\frac{1}{\sqrt{f}} \right) \ln \left(\left 2f(t - c) + 2\sqrt{f^2(t - c)^2 + fa} \right \right) + d$	a : maximum growth rate, c : age at which the growth rate is maximum, d : the body size at which the growth rate reaches a maximum, f : rate of change of growth rate.

2.6. Model Selection

The most plausible model was selected using the Bayesian Information Criterion [20], $BIC = 2 \cdot LL + \ln(n)K$, where $-LL$ is the negative log-likelihood, n is the total pairs of age-length data used, and K is the number of parameters in each model. The model having the lowest BIC value was chosen as the most plausible. Differences in BIC values $\Delta i = BIC_i - BIC_{min}$ were estimated for all models tested and the weight of evidence in favour of each model was estimated using the following equation [21]:

$$w_i = \frac{\exp\left(-\frac{1}{2}\Delta_i\right)}{\sum_{i=1}^{10} \exp\left(-\frac{1}{2}\Delta_i\right)} \quad (4)$$

3. Results

3.1. Growth

A total of 1390 individuals were measured in length over 40 days. The data showed how size disparity with age, both raw (Figure 1A) and daily averaged data (Figure 1B). The duration in days for each stage of the larval culture (Figure 1A) and the changes in the feeding regime throughout the culture (Figure 1B) are shown. These results support evidence of growth depensation in early stages of cultured totoaba and the increasing response of the growth rate and the variance in different stages of ontological development, as well as changes in food offered (Figure 1C).

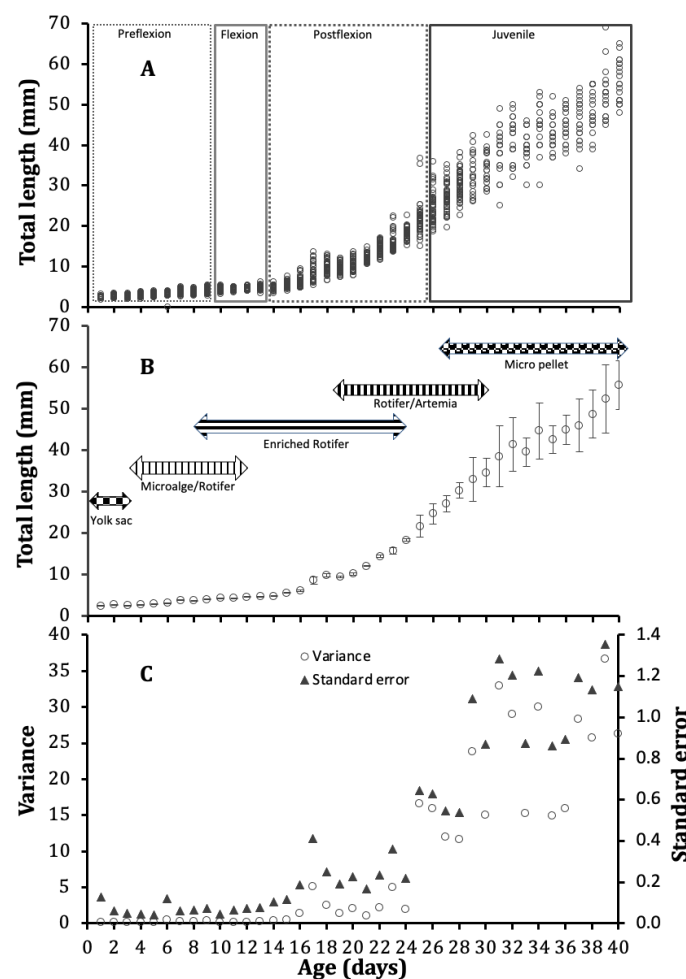


Figure 1. Total length during hatchery production of *Totoaba macdonaldi* according to age. (A) Raw data and development stage, (B) Average variation and feeding regime, (C) Length variance and standard error-at age.

3.2. Model Selection

The best model given the data was Exp-Schnute, which showed a sigmoid shape (Figure 2). We caution that even when this was the best model, data from the last two days (39- and 40-days post-hatching) could not be captured by this or any other model. The plausibility computed was 100% (Table 2); for comparison purposes, the most meaningful curves are presented (Figure 3). Only the Tanaka and Exp-Schnute fits showed sigmoid mean length-at age. Six models exhibited an exponential-like curve, and two models followed a power shape.

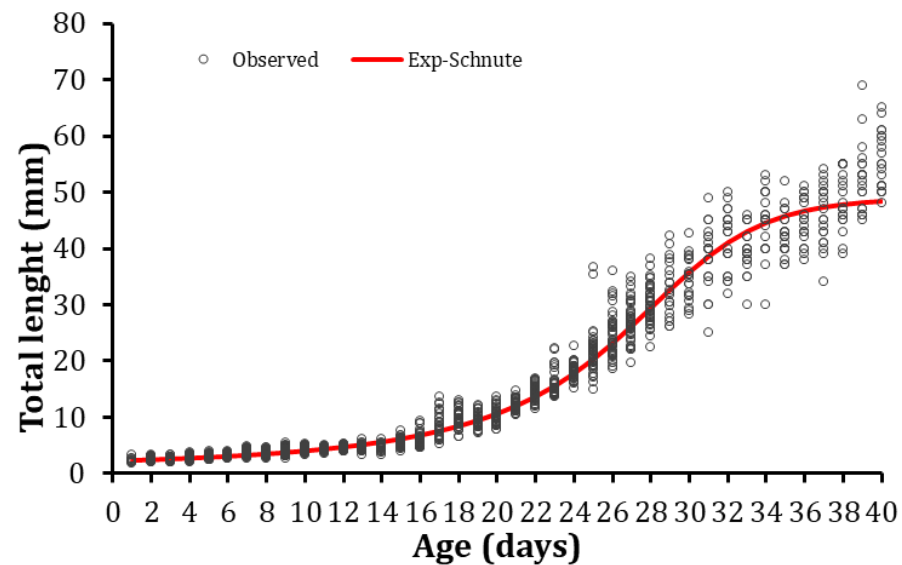


Figure 2. The best-fit model (Exp-Schnute) for observed growth of early stages of *Totoaba macdonaldi*.

Table 2. The Bayesian information criterion (BIC) for each of the ten models. Δ_i , differences in BIC; W_i , Bayesian weights.

Models	Parameters	BIC	Δ_i	W_i	Y1	Y2	A	b	c	d	F
EXP-Schnute 1	44	5052	0	1	0.88	3.88	0.37	−7.01	0	0	0
Persistence	43	5814	762	0	0	0	2.89	1.53	24.22	0	0
Tanaka	44	5837	785	0	0	0	0.02	0	25.08	37.95	0.04
Schnute 1	44	6487	1435	0	2.62	70.04	−0.42	4.40	0	0	0
Logistic	43	6707	1655	0	0.10	−1.00	1.82	62.49	0	0	0
Bertalanffy	43	6724	1672	0	2.14	69.61	−0.10	1.00	0	0	0
Schnute 4	42	6783	1753	0	1.94	67.06	0	0	0	0	0
Schnute 3	43	6790	1760	0	1.93	66.95	0	1.78×10^{-3}	0	0	0
Extended power	43	10,056	5003	0	0	0	2.63	0.53	−22.51	0	0
Power	42	16,743	11,691	0	0	0	0.13	1.52	0	0	0

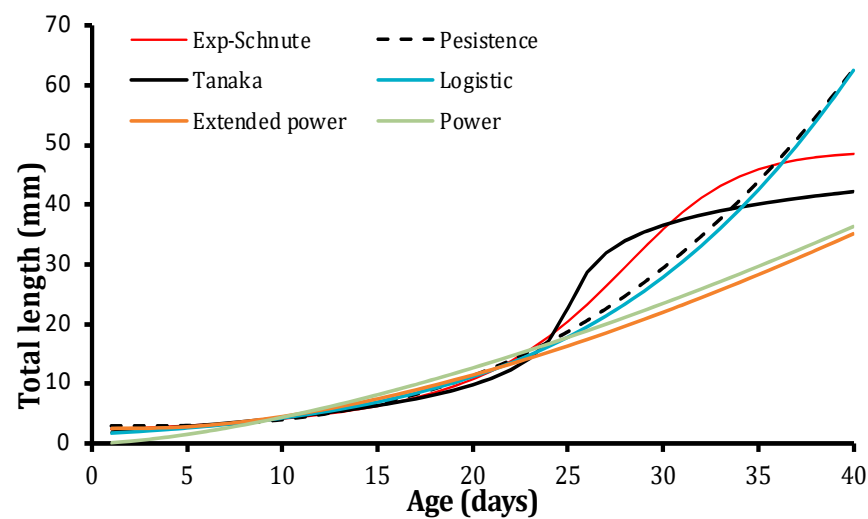


Figure 3. Trajectories of the most biologically meaningful models used to describe the growth of the *Totoaba macdonaldi* under laboratory conditions.

3.3. Growth from Literature

Figure 4 summarizes the growth data found in the literature; it shows the growth of early stages of totoaba under laboratory conditions with diverse objectives. The data are for different days post-hatching (DPH); the longest period was 45 DPH but started at 4 DPH [31]. One study was run only from 20 to 40 DPH [32] and growth resulted in a straight line. Larvae in three studies [31,33,34] and our data exhibited a similar growth until 14 DPH (Figure 4).

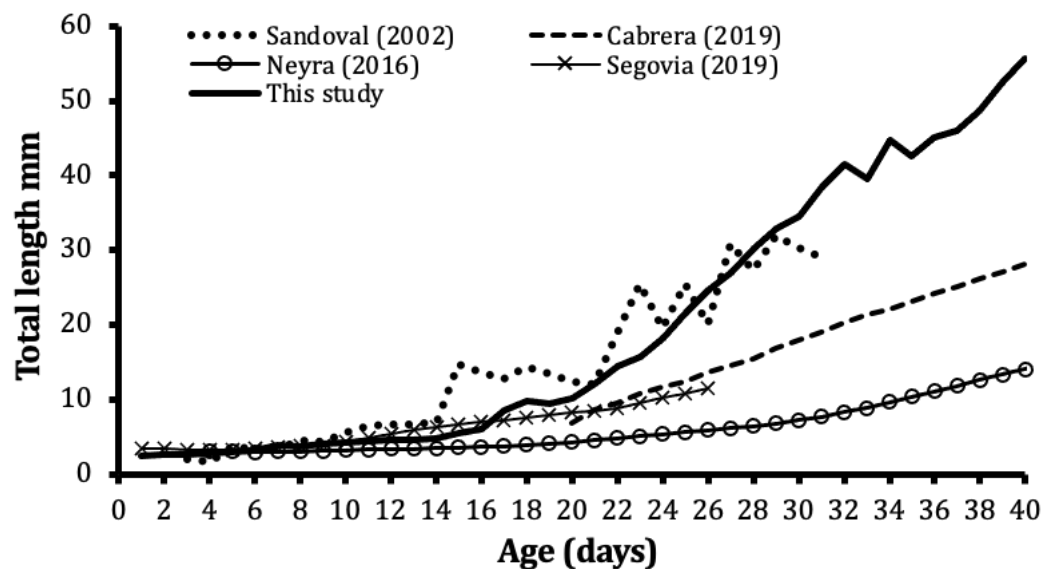


Figure 4. Growth of *Totoaba macdonaldi* early stages under laboratory conditions reported in different studies. Dotted line: [31]; line and circles: [29]; solid line: this study; broken line: [30]; line and squares: [32].

4. Discussion

Modelling growth of larval fish stages in culture conditions is not a common practice; most frequently, information used to record development is initial and final weight or length [34]. On occasions, studies show a graphic of growth (e.g., [35]). Reference [20] has shown that a more informative way to describe the growth patterns in cultivated organisms is to fit observed data to a model. This allows for accurate interpolation of

size at any time in the observation range, not just when the data were obtained (interpolations are not recommended without fitting a model). However, selecting the adequate model remains a complicated issue for many biologist; this is discussed in more detail in subsequent paragraphs.

There is no single report in peer reviewed or grey literature where growth is modelled for the larval stage for totoaba or any other fish species. The study of reference [36] includes a curve of growth in length and adds an exponential equation to the figure. Reference [37] divided the growth curve into two separate periods, the first from 0 to 16 days-post hatching (DPH) and a second from 17 to 45 DPH and describe each period with linear regression; these two studies are not very helpful to understand totoaba larval growth because, as shown here, growth is a smooth, continuous process. Our results show that the raw data described a power-like growth; a closer look suggested a sigmoid curve with two inflection points. Reference [38] studied the meagre *Argyrosomus regius* over 32 DPH. They suggested a quasi-sigmoid curve with two inflection points, the second at 30 DPH, similar to what was found in the present work. Our study indicates that the early stages of totoaba are best described by a sigmoid curve; this result might apply for sciaenid fishes in general. Further, reference [37] conducted a study on *Cursivas* during 45 DPH; they established a first period from 0 to 16 DPH and a second from 17 to 45 DPH. Both linear regressions yielded an r^2 over 0.95. In the present study with totoaba, we also studied these two periods separately, but we do not present the results. For the first period, from 1 to 16 DPH, a linear regression was obtained with $r^2 = 0.7425$ ($L = 0.2292 \times \text{DPH} + 1.9668$); for the second period, from 17 to 40 DPH, $r^2 = 0.9288$ ($L = 2.158 \times \text{DPH} - 31.152$). Results of reference [36] are similar to those in Figure 3 of the present study. Six models follow an exponential curve, but the best-fit model was the sigmoid shape Exp-Schnute.

Our results show that the early somatic growth of totoaba up to 38 days post-hatching (DPH) displays two inflexion points: between ca. 16–18 DPH, and ca. 31–33 DPH. These features were observed in the original data and are presented here for the first time and are also captured by the winning model (up to 38 DPH). The inflexion points may reflect the timing of a well-developed digestive tract in the larvae of fishes and as result the weaning success. Reference [35] conducted a study with totoaba that included the weaning at 17, 22 and 27 days-post-hatching (DPH). Between 3 and 5 DPH the totoaba larvae already have developed their digestive tract, and at 17 DPH larvae were weaned onto commercial diets. Furthermore, by 20–24 DPH larval totoaba have a completely functional and developed digestive system based on measured activity of the proteases trypsin, chymotrypsin, and pepsin [36]. In the present study, the formulated feed (weaning) started at 31 DPH; as result, the second inflection point was evident at 32–35 DPH. Empirical data suggests that at 36 DPH totoaba had completed weaning, whence larvae entered a new growth phase.

Sound model fit of empirical data is a desirable way to describe growth patterns in aquaculture [20]. This facilitates interpolation of growth at a given age within the observed range. Selecting the most plausible model is still challenging for some biologists. A single model such as von Bertalanffy growth function is most commonly used to estimate growth parameters of different cultivated fishes. However, contrasting multiple models has become common practice [9,17,24,27] addressing the question: which models must be considered, asymptotic, or non-asymptotic? For the spotted rose snapper (*Lutjanus guttatus*, Steindachner 1869) farmed in marine cages, [9] chose 10 models including asymptotic, non-asymptotic and bounded. To our knowledge, multiple growth models had not been tested for the early stages of any fish species.

Reference [28] introduced a generalized, versatile model to evaluate individual growth that can include many alternative equations and researchers further modified the Schnute model to describe a specific patterns of the species under study. In our case, only the Tanaka model was able to describe the growth data of totoaba larvae and juveniles. The new equation, called Exp-Schnute, not only improved the Tanaka model but also obtained the best performance. This modification captures the biological principle of growth acceleration: the equation resulted in a sigmoid-shaped growth curve with a larval period of accelerated

development followed by reduced growth rate. As mentioned, this seems to be related to a change from live to formulated feed. Albeit the proposed equation might generate discussion, our main objective is to provide a simple example whereby changing an existing growth model might yield comprehensive understanding of growth drivers. We expect that in future studies of early fish stages the Exp-Schnute be confronted with other growth models.

Size variability within individual fish of the same age may result of genetic differences in growth potential, or differential food accessibility. Fish weaning is considered a bottleneck to completely control a rearing biotechnology [36]. Dominant (larger or more active) fish can control access to food for “subdued” individuals; the former will display a better growth performance than the latter. Such differences in growth rate usually either rise or fade with age. Growth depensation will occur when growth potential accumulates in some or several individuals, so that larger fish will do better than smaller ones. Growth compensation will ensue if larger individuals reach a size limit and smaller fish catch-up in size. Constant growth-at age variability will result if depensation and compensation processes balance each other [39].

Most growth studies for either wild or cultivated animals assume constant variation-at-age and a priori fail to consider growth depensation or compensation when this might be a pervasive feature. Individual variability-at-age should be accounted to parametrize models for a better result [12]. This approach has been used both for wild fishes [8] and cultivated fishes [9], concluding that this must be a common practice. In the present study we used such approach; further insights and discussions are provided in references [8,9]. References [10,11] reported a very significant size disparity among fishes of the same age under cultured conditions for early stages of *L. guttatus*. In the present study with totoaba, individual variability increased with age, supporting the hypothesis of growth depensation as described by reference [12]. This justifies the model parametrization considering multiplicative error, depensation approach or observed variance as proposed by reference [8]. Considering observed variance resulted in the best parametrization as compared to alternative assumptions [8,9]. It is recommended that, at least for sciaenid fish, the density of the culture be reduced to avoid depensatory individual growth and prevent cannibalism.

Our model is a heuristic tool useful as it captures the main features observed in early totoaba larval growth data under the specific conditions that we used in our culture setting, except for the last two days, for which further analysis is needed. Our model captured two inflection points which might be related to physiological aspects of the species under our cultivation conditions. Further investigation is needed to ascertain if the growth observed in controlled conditions reflects early growth in wild totoaba, and whether this is driven by genetics or environmental aspects.

5. Conclusions

We highlight three important results of the present work: (1) the best model to describe the growth trajectory in the earliest stages of *Totoaba macdonaldi* in a farmed environment is a sigmoid-shaped curve. (2) The results support evidence of growth depensation in early stages of cultured totoaba and growth depensation leads to the application of a very high-performance objective function to analyze individual length-at-age variability. (3) Our data and model fitting indicate that early larval totoaba up to 38 days post-hatching (DPH) displays increasing length-at age variance and two inflexion points: the first between 16 to 18 DPH and the second between 31 to 33 DPH. Although explanations for increasing variance and the two inflexion points need further research, our results have meaningful practical implications for researchers and people interested in cultivating totoaba.

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