



# Age and multi-model growth estimation of white grunt, *Haemulon plumieri*, in the southern Gulf of Mexico from otolith macrostructure analysis

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## ABSTRACT

In the southern Gulf of Mexico fishery of the white grunt (*Haemulon plumieri*) has gained relevance as an alternative resource to fisheries considered in decay (e.g., red grouper); however, the extent of knowledge of the biology of this species in the region is scarce. Therefore, the aim of this study was to estimate the age and growth of white grunt under a multi-model approach (information theory). A total of 421 individuals were sampled monthly on the continental shelf of Yucatan from September 2015 to August 2016. Five growth models were evaluated through a multi-model approach. Periodicity of growth zones was annual according to the marginal index. Maximum estimated age was 17 years and 90% of the specimens were under 8 years of age. Models that best explained the growth of white grunt were asymptotic without an evident inflexion point (Johnson and von Bertalanffy models). The first growth estimate of this species in the southern Gulf of Mexico is reported with this approach, contributing elements to improve evaluations in future studies.

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## 1. Introduction

Overexploitation of fishery resources of high commercial value has caused fishermen to be oriented to catch species previously considered as unprofitable or of low quality (Salas et al., 2006). Currently, this activity is carried out on the Campeche Bank in the southern Gulf of Mexico (SGM) due to the considerable decrease in catches of historically relevant resources for the fisheries of the region (e.g., red grouper; DOF, 2018). In an ecological sense, these resources perform a key role in the structure and operation of the marine ecosystem (Pauly and Palomares, 2005); an example of this is white grunt (*Haemulon plumieri*) (Lacepède, 1801). One of its functions in the ecosystem is to be an importer of energy towards reef area communities, as it is prey of species of larger size (Darcy, 1983). In economic terms, in various countries (including the Gulf of Mexico and the Caribbean Sea) the white grunt is a relevant component of small-scale and recreational fishing (Poot-López et al., 2018).

White grunt displays a wide distribution in the western Atlantic Ocean, from the United States to Brazil (Darcy, 1983). This species is generally found in coastal waters associated with coral

reefs, seagrass beds and rocky bottoms (García et al., 2010) and inhabits areas with depths ranging from 5 to 25 m (Estrada, 1986). In the SGM, this resource is mainly captured by small-scale fleets whose fishing is linked to various fish species (e.g., seranids and snappers). White grunt is available to fishermen throughout the year (Salas et al., 2006).

In the last four decades, white grunt has acquired relevance as a fishing source in the SGM (Mexicano-Cíntora et al., 2009). During this period, its catches have shown fluctuations ranging from 89 to 333 t (1994 and 1998, respectively) (Mexicano-Cíntora et al., 2007). Catches have remained above 550 t since 2005, almost reaching 1000 t in the 2009–2014 period (CONAPESCA, 2018). These production levels exceeded the objective reference point (maximum sustainable yield, MSY) estimated for this species in the region, of 255 t (Mexicano-Cíntora et al., 2007); therefore, it is probable that this resource is subject to intense exploitation, which could lead to an undesirable state for its fishery (overexploitation). In spite of the above, the white grunt fishery in the SGM is carried out without an established regulation scheme, since knowledge about its biology and population dynamic is scarce and insufficient to generate adequate management strategies.

Studies of the white grunt in the SGM have addressed subjects such as individual growth through length frequencies

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(Domínguez-Viveros and Avila-Martínez, 1996), length-weight relationship (Poot-López et al., 2018) and differentiation among populations (Villegas-Hernández et al., 2014). In other regions of the Atlantic Ocean, including the Gulf of Mexico and the Caribbean Sea, there have been age estimates of white grunt through reading of annuli in hard structures (i.e., otoliths) (Padgett, 1997; Potts and Manooch, 2001; Murie and Parkyn, 2005; Araújo and Martins, 2007; Vasconcelos-Filho et al., 2018) while for the SGM this information is non-existent.

The use of mathematical equations to represent and simplify the growth of fish is essential to obtain base information to be used in stock assessment models. The von Bertalanffy model (VBGF; von Bertalanffy, 1938) is the one most used in fisheries science (Grosjean, 2001); however, several authors have expressed that occasionally this model does not adequately describe the relationship between age and length because some species could have different growth patterns (Katsanevakis and Maravelias, 2008). For this reason, the use of multi-model inference, which comes from information theory, has been suggested, given that it helps determine the equation that best explains statistically the growth pattern of a given species or provides a greater number of alternatives to model the length-age relationship (Burnham and Anderson, 2002; Katsanevakis, 2006).

There are currently alternative growth models (including VBGF) that can compete in determining which equations are statistically more robust (Katsanevakis and Maravelias, 2008). The above has not been tested in species such as white grunt; consequently, the uncertainty level involved in assuming *a priori* that VBGF is the equation that explains the growth of this species is unknown. Comparison of different candidate models of this resource is relevant; it will allow more robust information of growth patterns and an adequate understanding of this important aspect of its biology.

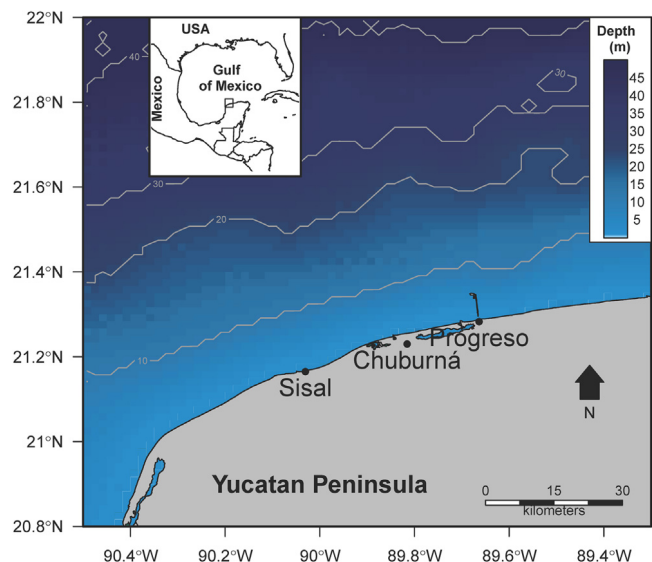
The aim of the present study was to estimate age through readings of otolith annuli, as well as to determine the growth pattern of white grunt (*Haemulon plumieri*) based on information theory (Burnham and Anderson, 2002). This was carried out in a region of the SGM where this resource is exploited but its biological information is scarce, and ages estimates through macrostructures are non-existent.

## 2. Material and methods

### 2.1. Field work and study area

Monthly samplings independent of commercial fishing were carried out on the continental shelf of the central coast of the Campeche Bank in the SGM (Fig. 1), which is characterised as a vast shelf where three climatic periods predominate: dry season (March–June), rainy season (July–October) and the ‘nortes’ season, named after the strong north winds but with little rain (November–February) (Mexicano-Cíntora et al., 2007).

The study was conducted from September 2015 to August 2016. Fish were collected during daylight hours by hook and line (numbers 8/10, 10/0 and 14/0), using squid tentacles (*Dosidicus gigas*) as bait. Total length (TL,  $\pm 0.1$  cm) and total weight (TW,  $\pm 0.1$  g) were recorded for each specimen. Similarly, sagittal otolith pairs from the sacculus were extracted from each fish to be later washed with running tap water and then stored in bags in distilled water. Samplings were carried out in rocky reef and sandy bottom areas with the aim of covering the total bathymetric distribution (between 2 and 25 m) of the reported abundance and thus cover a larger range of possible sizes of white grunt (Estrada, 1986).



**Fig. 1.** Study area of the white grunt (*Haemulon plumieri*) located in the southern Gulf of Mexico. Samplings were carried out in front of the Chuburná port from 5 to 25 m deep.

### 2.2. Laboratory work

The left otoliths were used for further processing since most of them showed less damage than the right otoliths. Otoliths were fixed in synthetic resin to subsequently obtain a central section approximately 1 mm thick via a low-speed cutter equipped with a diamond-tipped disc (Buehler Isomet). The otolith sections were fixed in slides for further analysis on the stereoscope (through reflected light). In order to decrease processing time and improve vision and reading of the growth zones in the otoliths, a methodology adapted from Easey and Millner (2008) was employed, which consisted of decalcifying and dyeing the sectioned otoliths by submerging them for 20–30 min in a 100 ml distilled water solution of 2.5 g of neutral red colouring, 0.5% ethanoic acid (glacial acetic acid) and 1 g of sodium chloride. After reaction, excess colouring was removed with running tap water.

Digitalised images of each sample were obtained to ease the reading of growth zones by reflected light with a stereoscope equipped with a 6 MP camera. Distances between the nucleus and growth zones based on a transverse plane and including the otolith radius (OR) were obtained with ImageJ software (Abramoff et al., 2004). In this work, a growth zone (age) is defined as the combination of an opaque and a translucent zones (Campana, 2001).

The type of otolith edge (opaque or translucent) was recorded with the aim of determining seasonality in the formation of the annuli of each sample. Finally, in order to determine the number of growth zones, sectioned otoliths were analysed by two independent readers at different times. When there was disagreement between the readers regarding the number of annuli, samples were read again until a consensus was reached. The OR–TL relationship was evaluated with five types of models (linear, Power, Logarithmic, Exponential and Polynomial). To determine which equation best describes the OR–TL relationship we used the determination coefficient ( $r^2$ ) criterion (Sokal and Rohlf, 2012).

### 2.3. Total length–total weight (TL–TW) relationship

The TL–TW relationship was estimated through the power equation proposed by Ricker (1975):  $TW = \alpha TL^\beta$ , where  $\alpha$  is

the intercept and  $\beta$  is the slope, also known as the allometry coefficient. The estimation of  $\alpha$  and  $\beta$  parameter were carried out by a linear regression analysis after log(TL)–log(TW) transformation. Likewise, 95% confidence intervals (CIs) of  $\alpha$  and  $\beta$  were estimated. The power of regression adjustment was evaluated by the determination coefficient ( $r^2$ ) (Sokal and Rohlf, 2012).

#### 2.4. Precision and validation of age

Precision of the age readings by both readers was analysed using the average percentage error (APE, Beamish and Fournier, 1981), which is defined by the equation:

$$APE = \frac{100}{n} \left[ \frac{1}{R} \sum_{j=1}^{R_i} \frac{|x_{ij} - \bar{x}_i|}{\bar{x}_i} \right] \quad (1)$$

where  $n$  is the number of analysed otoliths,  $R_i$  is the number of readings for otolith  $i$ ,  $x_{ij}$  is the number of read annuli in otolith  $i$  by the reader  $j$ , and  $\bar{x}_i$  is the calculated average age of otolith  $i$ .

The coefficient of variation (CV) proposed by Chang (1982) was employed to verify the consistency of the values of APE by the following formula:

$$CV = \frac{100}{n} \left[ \sum_{i=1}^n \left( \frac{sd_i}{\bar{x}_i} \right) \right] \quad (2)$$

where  $sd_i$  is the standard deviation of the measured ages by both readers for otolith  $i$ . Additionally, an age-bias plot and test for bias was included ( $\chi^2$ , 95% confidence intervals) in order to compare readers' estimates (McBride, 2015).

Once the reading precision was calculated, the periodicity of the formation of growth zones was validated by using an analysis of the proportion of edge type on the otolith (translucent and opaque) and marginal index (MI). The value of MI was estimated for each organism through the equation (Panfili and Morales-Nin, 2002):

$$MI = AMD/D_{i,i-1} \quad (3)$$

where AMD is the absolute marginal distance that separate the last growth mark from edge and  $D_{i,i-1}$  is the distance that separate the last two growth marks.

#### 2.5. Growth

Growth pattern of white grunt was determined through five candidate models that were compared by means of a multi-model approach based on information theory (Burnham and Anderson, 2002). These five compared candidate models were: von Bertalanffy (VBGF; von Bertalanffy, 1938), Gompertz (Gompertz, 1825), Logistic (Moreau, 1987), Richards (Richards, 1959) and Johnson (Ricker, 1979). The definitions of the parameters from each model are given in Table 1.

Parameters ( $\theta_i$ ) of the growth model  $i$  were estimated through a non-linear setting using the Newton algorithm (Kutner et al., 2005). The quadratic sum of the error ( $\varepsilon$ ) of each model was minimised, assuming that  $\varepsilon_i \sim N(0, \sigma^2)$ . Settings were performed by the base package (nls function) of the programming language R (R Core Team, 2018).

The choice of model that best described the growth of white grunt was made with Akaike information criterion ( $AIC_c$ ) fitted for smaller sample sizes (Burnham and Anderson, 2002) through the following equation:

$$AIC_{c,i} = AIC_i + \frac{2\theta_i(\theta_i + 1)}{n - \theta_i - 1} \quad (4)$$

for least squares:

$$AIC_i = n \left[ \log \left( 2\pi \frac{RSS_i}{n} \right) + 1 \right] + 2\theta_i \quad (5)$$

where  $\theta_i$  is the number of parameters from model  $i$ ,  $RSS_i$  is the quadratic sum of error for model  $i$  and  $n$  is the number of observations. Differences of AIC ( $\Delta_i$ ) were estimated from  $\Delta_i = AIC_{c,i} - AIC_{min}$ , where the lowest value of AIC ( $AIC_{min}$ ) was chosen as the best model (Burnham and Anderson, 2002). If  $\Delta_i > 10$ , models were considered to be without statistical support and thus should not be taken into account; if  $4 < \Delta_i < 7$ , models showed partial statistical support; and if  $\Delta_i < 2$  they showed good statistical support and are thus proposed for use in this species (Luquin-Covarrubias et al., 2016).

In order to quantify evidence in favour of the best model, weights of Akaike were estimated ( $w_i$ ) through the following formula:

$$w_i = \frac{e^{-0.5\Delta_i}}{\sum_{i=1}^5 e^{-0.5\Delta_i}} \quad (6)$$

The average asymptotic TL of the model  $i$  ( $\overline{TL}_\infty$ ) was estimated through the equation:

$$\overline{TL}_\infty = \sum_{i=1}^5 w_i TL_\infty \quad (7)$$

For each value of  $\overline{TL}_\infty$ , the standard unconditional error was estimated (Katsanevakis and Maravelias, 2008):

$$SE(\overline{TL}_\infty) = \sum_{i=1}^5 w_i \left[ \text{var} \left( \frac{TL_\infty}{g_i} \right) + (TL_\infty - \overline{TL}_\infty)^2 \right]^{1/2} \quad (8)$$

where  $\text{var}(\frac{TL_\infty}{g_i})$  is the variance of the observed data of each candidate model.

Finally, the confidence interval (95%) was estimated through the following equation:

$$TL_\infty \pm t_{df, 0.975} SE(\overline{TL}_\infty) \quad (9)$$

### 3. Results

#### 3.1. TL–TW relationship

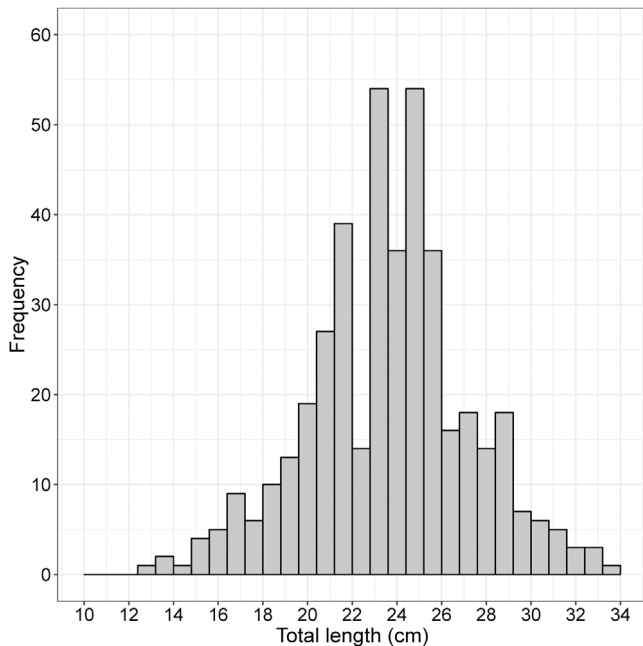
A total of 421 specimens of white grunt were collected. 242 males and 113 females were registered in the captures, although the sex of 66 specimens was not determined. It was not possible to carry out the analyses by sexes due to the low representativeness in sample size and range of sizes of the females. The monthly average sample size was 35 organisms ( $\pm 11$  SD) with TLs that varied between 13.0 and 33.5 cm TL ( $23.7 \pm 3.3$  cm mean SD; Fig. 2). Parameters of the TL–TW relationship corresponded to  $\alpha = 0.029$  (CI: 0.023–0.036) and  $\beta = 2.798$  (CI: 2.725–2.871). The fitted model was highly significant with  $r^2 = 0.93$  ( $F_{1,419} = 6361$ ,  $P < 0.001$ ; Fig. 3a). The value of  $\beta$  was statistically lower than the isometry value ( $\beta = 3$ ); therefore, white grunt showed a type of negative allometric growth ( $t$ -test = 8.670,  $P < 0.05$ ).

#### 3.2. Age

Annuli were formed by wider opaque zones alternated with translucent zones (Fig. 4). Observed ages of white grunts ranged from 0–17 years. Analysis of the growth reading precision indicated a consistency between both readers (Chi-test;  $\chi^2 = 2.20$ ,  $P > 0.05$ ), with low APE and CV values (5.32% and 7.53%, respectively) (Fig. 5). Fish that did not have the first fully formed growth annuli were assigned an age of zero years. The most

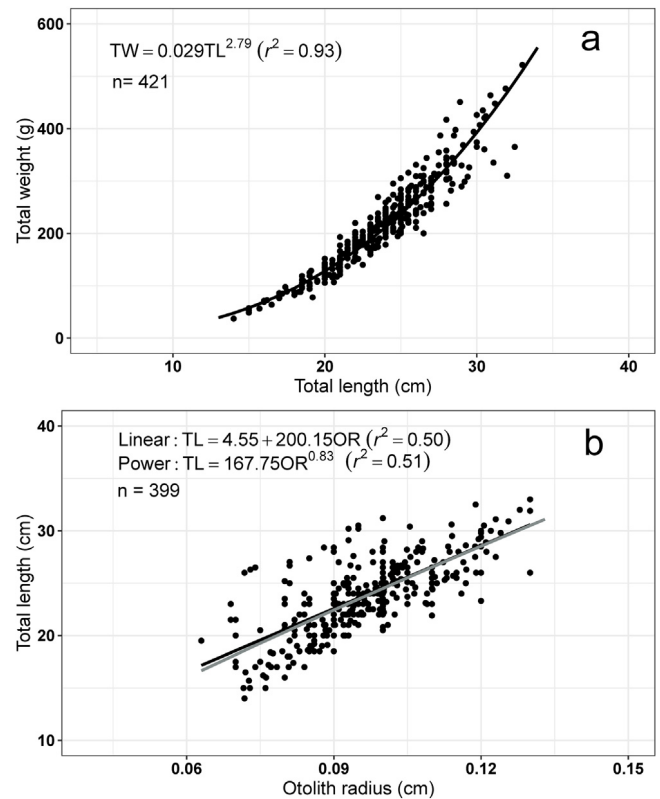
**Table 1**Candidate growth models applied to total length-at-age data of white grunt (*Haemulon plumieri*) in southern Gulf of Mexico.

Model	Equation	Parameters	Model description
von Bertalanffy (VBGF)	$TL_t = TL_{\infty} [1 - e^{-k(t-t_0)}]$	$TL_t$ is the total length at age $t$ ; $TL_{\infty}$ is the maximum (asymptotic) total length; $k$ is the growth coefficient and $t_0$ is the age at the 0 theoretical total length.	Fast growth in its first phases which decreases until reaching the asymptotic length in adult ages (von Bertalanffy, 1938)
Gompertz	$TL_t = TL_{\infty} e^{\left[ -e^{-k(t-t_0)} \right]}$	$TL_{\infty}$ is the maximum (asymptotic) total length; $k$ is the growth coefficient in the inflection point; $t_0$ is the age at the inflection point.	Exponential growth in the first ages with inflection point, decreasing the growth in adult ages (Gompertz, 1825).
Logistic	$TL_t = \frac{TL_{\infty}}{1 + e^{-k(t-t_0)}}$	$TL_{\infty}$ is the maximum (asymptotic) total length; $k$ is the growth coefficient in the inflection point; $t_0$ is the age at the inflection point.	Curve with an exponential growth in the first ages, inflection point and logarithmic growth in advanced ages (Moreau, 1987).
Richards	$TL_t = \frac{TL_{\infty}}{[1 + e^{-kt + \gamma}]^{\delta}}$	$TL_{\infty}$ is the maximum (asymptotic) total length; $k$ is growth coefficient at inflection point; $\gamma$ and $\delta$ are non-dimensional parameters	Curve that can acquire different forms according to the value of $\delta$ , its turning point could be located anywhere in the curve (Richards, 1959)
Johnson	$TL_t = TL_{\infty} e^{-\left[ \frac{1}{k}(t-t_0) \right]}$	$TL_t$ is the total length at age $t$ ; $TL_{\infty}$ is the maximum (asymptotic) total length; $k$ is the growth coefficient and $t_0$ is the age at the 0 theoretical total length.	Asymmetric curve with sigmoid shape and a point of inflection very low or close to zero (Ricker, 1975)

**Fig. 2.** Structure of total lengths of white grunt (*Haemulon plumieri*) catches collected in the southern Gulf of Mexico.

representative age groups from the samplings were those under 8 years, representing 91% of the total sampling, fish of 3–6 years being the most frequent. The least represented fish were the ones of older age (> 8 years).

The OR varied between 0.06 cm and 0.13 cm (mean  $0.09 \pm 0.01$  cm SD) corresponding to 19.50 cm and 33.00 cm TL fish, respectively. According to the  $r^2$  the best models that described the OR–TL relationship were Power  $TL = 167.75 \times OR^{0.83}$  ( $r^2 = 0.51$ ,  $F_{1,392} = 412.3$ ,  $P < 0.001$ ; Fig. 3b) and Linear  $TL = 4.55 + 200.15 \times OR$  ( $r^2 = 0.50$ ,  $F_{1,392} = 401.8$ ,  $P < 0.001$ ; Fig. 3b). The comparison between the mean of the better models did not show a significant difference ( $t$ -test = 1.19,  $P > 0.05$ ). The model which described the OR–TL relationship was  $TL = 4.55 + 200.15 \times OR$ , being highly significant ( $r^2 = 0.50$ ,  $F_{1,392} = 401.8$ ,  $P < 0.001$ ; Fig. 3b). The monthly analysis of MI and otolith edge type showed an annual peak in October and November, indicating the

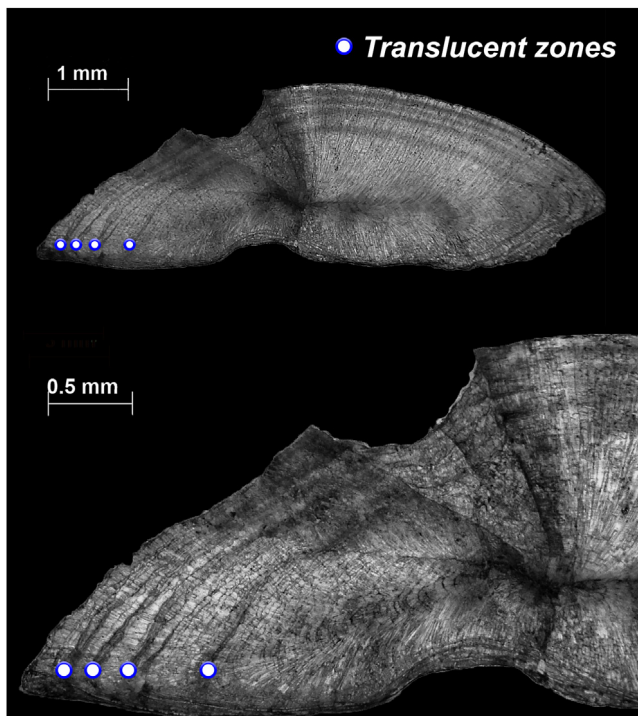
**Fig. 3.** (a) Total length–total weight relationship (TL–TW) and (b) otolith radius–total length relationship (OR–TL), grey line is the power model and black line is linear model.

formation of a group of opaque and translucent zone during the year (Fig. 6).

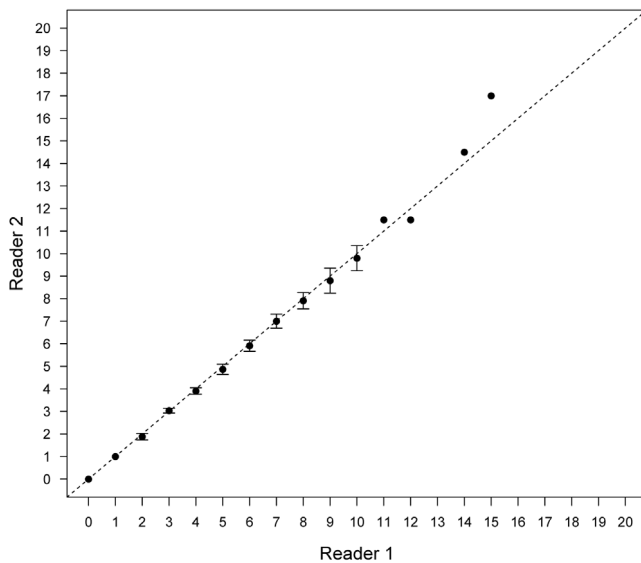
### 3.3. Growth

Growth parameters and CIs of the five candidate models, as well as the behaviour of fitted curves in regard to the observed values, are summarised in Table 2 and curves in Fig. 7. The model with lowest  $AIC_c$  was Johnson ( $AIC_c = 2094.97$ ) with a  $w_i$  in favour of 37.87% (Table 3) followed by von Bertalanffy's model ( $w_i = 26.06\%$ ); both models showed growth parameters



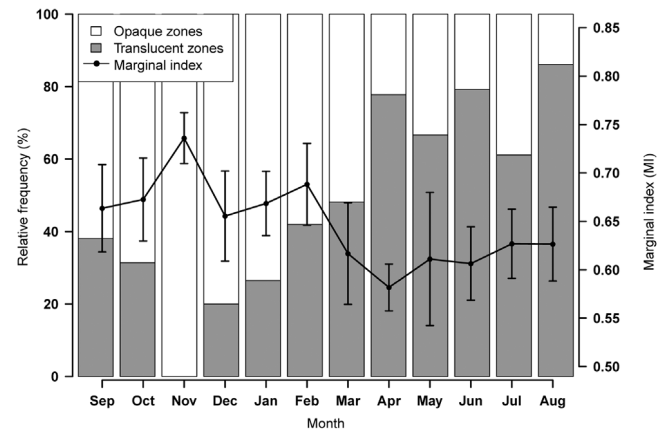


**Fig. 4.** Otolith section under reflected light (Mann-Lang and Buxton, 1996): the white points.

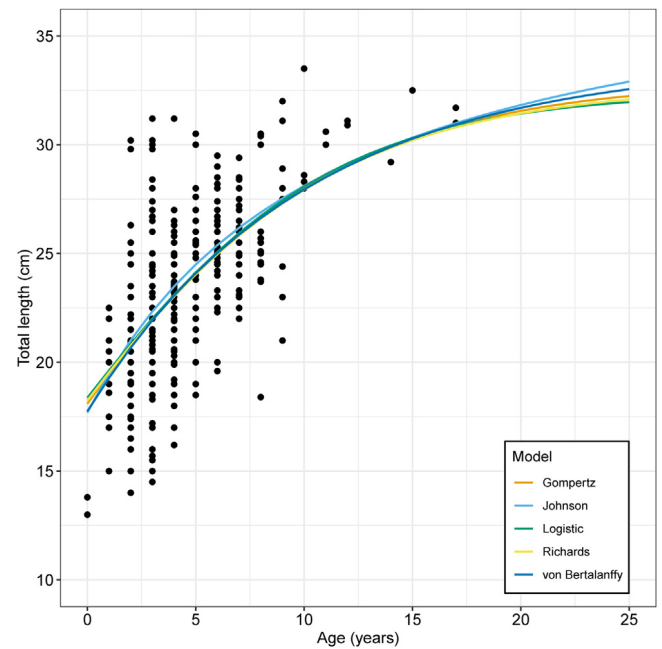


**Fig. 5.** Mean (points) and 95% confidence intervals between readers estimated for of white grunt (*Haemulon plumieri*). The dashed grey line represents age estimates that agree. No statistical differences were found between both readings (Chi-test;  $\chi^2 = 2.20$ ,  $P > 0.05$ ). indicate the translucent zones of an individual of white grunt (*Haemulon plumieri*).

values that were consistent with those reported in the literature (e.g. Ramos and Pozo, 1984; Murie and Parkyn, 2005; Araújo and Martins, 2007). The VBGF and Gompertz models displayed a good statistical support, all of them with values of  $\Delta_i < 2$ , while the Logistic and Richards model showed the lowest statistical support ( $\Delta_i > 2$ ; Table 3). Of the compared models, those that lacked an evident inflection point (Johnson and VBGF) were the ones that better explained the growth pattern of white grunt.



**Fig. 6.** Relationship among monthly behaviour of opaque and translucent zones and marginal index (MI)  $\pm$  standard deviation of white grunt (*Haemulon plumieri*) catches in the southern Gulf of Mexico.



**Fig. 7.** Growth pattern of white grunt (*Haemulon plumieri*) catches in the southern Gulf of Mexico. The behaviour of the five confronted models is shown. The best model was Johnson followed by von Bertalanffy (VBGF) model.

#### 4. Discussion

This study contributed relevant and actualised information on the estimation of age and growth parameters of white grunt in the SGM. For the first time, different growth models for this resource were compared based on information theory through a multi-model approach (Burnham and Anderson, 2002).

The TL range was found to be similar to values recorded for this species in adjacent areas (Kapote, 1971; Domínguez-Viveros and Avila-Martínez, 1996), suggesting that this work covered most of the sizes present at the study area. In this study, the recorded sizes were evidently smaller than those recorded in other regions, such as Brazil (Araújo and Martins, 2007) and the United States (Murie and Parkyn, 2005). These differences could be attributed to external factors, such as local environmental characteristics, genetic aspects, competitive interactions and/or fishing pressure, which is generally focused in the catch of large sized organisms (Law, 2000).

**Table 2**  
Growth parameters, confidence intervals (in parenthesis) and unconditional standard error  $SE(\overline{TL}_{\infty})$  estimated for white grunt (*Haemulon plumieri*) in southern Gulf of Mexico.

Model	Growth parameters					$SE(\overline{TL}_{\infty})$
	$TL_{\infty}$ (cm)	$k$ (yr <sup>-1</sup> )	$t_0$ (years)	$\gamma$	$\delta$	
von Bertalanffy (VBGF)	33.88 (30.36–37.39)	0.10 (0.03–0.18)	–7.42 (–12.96 to –4.42)			1.14
Logistic	32.41 (30.02–34.81)	0.16 (0.09–0.24)	–1.68 (–2.57–1.40)			0.77
Gompertz	33.00 (30.18–35.81)	0.13 (0.06–0.21)	–3.92 (–5.25 to –2.22)			0.91
Richards	32.73 (26.93–38.53)	0.14 (–0.07–0.63)		–1.24 (–3.32–4.92)	2.30 (0.08–16.19)	0.29
Johnson	39.47 (34.48–44.45)	0.17 (0.05–0.36)	–7.33 (–15.90–3.59)			6.01
Model average	34.55 (16.58–52.51)					9.13

**Table 3**  
Analysis of the five candidate growth models for white grunt (*Haemulon plumieri*) in southern Gulf of Mexico, which show the number of parameters ( $\theta$ ), the Akaike information criterion ( $AIC_c$ ), the Akaike differences ( $\Delta_i$ ), the Akaike weight percentage ( $w_i$ ).

Model	$\theta$	$AIC_c$	$\Delta_i$	$w_i$ (%)
Johnson	3	2094.97	0.00	37.87
von Bertalanffy (VBGF)	3	2095.72	0.74	26.06
Gompertz	3	2096.46	1.49	17.92
Logistic	3	2097.16	2.19	12.66
Richards	4	2098.83	3.86	5.48

The estimated value of the allometry coefficient was  $\beta = 2.798$ , a value within the range that is generally accepted for fish ( $2.50 < \beta < 3.50$ ) (Froese, 2006). The values of parameters  $\alpha$  and  $\beta$  of LT-WT regression, coincide with the ranges reported in Brazil (Vasconcelos-Filho et al., 2018). The value variations of parameter  $\alpha$  are due to the use of different units of measurement of LT cm (Shinozaki-Mendes et al., 2013; Viana et al., 2016; Vasconcelos-Filho et al., 2018) or mm (Murie and Parkyn, 2005). Negative allometric growth is common in this species (Murie and Parkyn, 2005) and suggests that the fish gains proportionally more total length than weight. Some authors have demonstrated that white grunt specimens tend to show a negative allometric growth when the sample is strongly biased towards juveniles (Potts and Manooch, 2001; Shinozaki-Mendes et al., 2013). This aspect must be considered, since the most part of the sampled organisms in this study were juveniles, pre-adults and young adults, given the shortage of mega-spawners in the study area. These were our results even though different numbers of hooks were used, thus covering the most part of the bathymetric distribution where most of the abundance of this resource is reported (Estrada, 1986). To date, the hypothesis of a possible segregation by size both bathymetric and longitudinally has not been tested in the SGM.

The determination coefficient estimated between the regression of OR–TL has been one of the highest recorded for this species ( $r^2 = 0.51$ ) and can be evaluated with both power and linear models, suggesting a correlation between the size of otolith and fish. In other distribution areas of white grunt, lower  $r^2$  values than those assessed in this study were estimated ( $<0.50$ ) (e.g. Padgett, 1997; Araújo and Martins, 2007), indicating that our case study is reliable in the use of otolith as an age and growth indicator of this fish.

Overall, the formation of growth annuli in white grunt was annual, based on the combined formation of translucent zone (dark zone) and opaque zone (white zone) (Fig. 6). This formation of annuli pattern is common in white grunt (Padgett, 1997;

Araújo and Martins, 2007). Months with peaks of translucent zones coincide with the period of higher temperatures: periods that are characterised by a slow growth of fish and a decrease in their metabolic rate (Morales-Nin and Ralston, 1990); while the months where there was a higher proportion of opaque zones formation coincided with lower temperatures, which are generally periods of fast growth of fish and metabolic energy is concentrated in somatic growth (Beckman, 1995). Some authors reported that the translucent zones converge with the spawning peaks of *H. plumieri* (Padgett, 1997; Murie and Parkyn, 2005; Shinozaki-Mendes et al., 2013). In the Yucatan Peninsula, Solís-Flores (2017) found that the spawning season of *H. plumieri* occurs from March to August, coinciding with the period of highest proportion of translucent zones and lowest MI values found on the present study.

The maximum estimated age for white grunt in the present study (17 years) was the lowest recorded for this species in comparison to other regions; e.g., 27 years in the United States (Padgett, 1997) and 28 years in Brazil (Araújo and Martins, 2007). Additionally, organisms showed TLs smaller than those of individuals from other areas but of the same age (i.e., Potts and Manooch, 2001). Different authors have reported that in regions of North America, it appears that white grunt population is mainly composed of individuals aged 8 years (Potts and Manooch, 2001), differing from regions of South America where specimens older than 8 years are the most abundant in the population (i.e., Brazil, Araújo and Martins, 2007).

All the previous work assumes that VBGF is the best option to describe the growth pattern of white grunt (i.e., Cuba, Ramos and Pozo, 1984; United States, Murie and Parkyn, 2005; Brazil, Araújo and Martins, 2007). This leads us to a greater uncertainty when describing the growth path for this species (Takane, 1987). Thus, in the present study, thanks to the multi-model approach (based on information theory) more than one hypothesis for the growth pattern of this species was tested, and it was demonstrated that asymptotic models are suitable for the use of this resource.

Although model that displayed a marked inflection point were statistically adequate (i.e., Gompertz;  $\Delta_i < 2$ ), all of them had negative  $t_0$  values, making them biologically unrealistic model, consequently, suggesting not to use sigmoid models to describe the growth pattern (e.g. Gompertz and Logistic models) of white grunt in future studies. This because the inflection point should occur during the natural history of the fish, since it can be determined by ontogenetic changes throughout the life cycle of the species, mainly fitting to individuals of high longevity (Carlson and Baremore, 2003).

On the other hand,  $TL_{\infty}$  is an important parameter in the growth curves and could be influenced by the scarce or null

**Table 4**Comparison of the estimated growth parameters (von Bertalanffy and Johnson models) in different regions of the white grunt (*Haemulon plumieri*) distribution.

Region	Sex	$TL_{\infty}$ (cm)	$k$ ( $\text{yr}^{-1}$ )	$t_0$ (years)	Authors
Northeast Florida, U.S.A.	Male	37.0	0.32	−0.36	Padgett (1997)
	Female	33.4	0.35	−0.70	Padgett (1997)
Carolinas, Florida, U.S.A.	All	59.1	0.08	−4.21	Potts and Manooch (2001)
Southeast Florida, U.S.A.	All	32.7	0.19	−4.21	Potts and Manooch (2001)
Florida, U.S.A Gulf of Mexico	Male	34.5	0.41	−0.85	Murie and Parkyn (2005)
	Female	31.7	0.35	−1.68	Murie and Parkyn (2005)
Brazil	All	31.2	0.48	−0.32	Araújo and Martins (2007)
Brazil	All	31.1	0.1	−4.7	Vasconcelos-Filho et al. (2018)
Southern Gulf of Mexico	All (VBGF model)	34.2	0.09	−7.61	Present study
Southern Gulf of Mexico	All (Johnson model)	40.2	0.15	−7.80	Present study

presence of information about adults and mega-spawners (Campana, 2001; Carmo et al., 2018). The  $TL_{\infty}$  in VBGF was low in comparison to those reported in the few works carried out in adjacent areas (Domínguez-Viveros and Avila-Martínez, 1996), while the Johnson model showed a higher  $TL_{\infty}$ , approaching the maximum TL recorded for this species (Froese and Pauly, 2018;  $TL = 53.0$  cm). The average lifespan ( $A_{95} = t_0 + 2.966/k$ ) defined as the age at which white grunt reaches the 95% of  $TL_{\infty}$  ( $\approx$  fish longevity) (Taylor, 1958) was of 17.22 years for the Johnson model and 25.34 years for the VBGF model. The only length at first maturity estimated in the study area corresponds to a  $TL = 15.17$  cm (Solís-Flores, 2017), which is equivalent to ages under two years. Therefore, the results of this study suggest that white grunt in the sampled area matures at early ages.

With regard to the growth coefficient, individuals of white grunt in the SGM showed  $k$  values (i.e.,  $k = 0.10 \text{ yr}^{-1}$  for VBGF and  $k = 0.17 \text{ yr}^{-1}$  for Johnson) within the reported range for this species along its distribution (Ramos and Pozo, 1984; Murie and Parkyn, 2005; Araújo and Martins, 2007) ( $0.08 \leq k \leq 0.71 \text{ yr}^{-1}$ ) even though our estimates of  $k$  were overall lower than those reported in previous studies, which suggests that white grunt of the SGM have slower growth and thus this species takes more time to reach its  $TL_{\infty}$  ( $>10$  years) (Table 4). In this sense, Araújo and Martins (2007) have pointed out that the high variability in estimates of the growth parameters, even when dealing with the same species but in different regions, could be attributed to multiple factors including the estimation method and adaptations to local environmental conditions.

Results obtained in this study indicate that according to the multi-model approach, the growth pattern of white grunt must be explained by asymptotic equations (i.e. Johnson and VBGF) rather than with sigmoid models. This allows the conclusion that this species shows a slow growth rate, which makes it susceptible to overexploitation. With this under consideration, authors such as Froese and Pauly (2018) catalogue this species as highly vulnerable, which is why it is necessary to establish urgent management and conservation policies for this resource. Lastly, there are reasons why white grunt individuals reach lower TLs at the same age in comparison with populations of the rest of the distribution region. These causes should be addressed in more detail in future work.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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