Age and growth of *Aplodinotus grunniens* (Perciform: Sciaenidae) in the mid-Usumacinta River

Edad y crecimiento de *Aplodinotus grunniens* (Perciforme: Sciaenidae) en la porción media del Río Usumacinta

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ABSTRACT. *Aplodinotus grunniens* represent a crucial artisanal fishery in the Usumacinta River's middle basin that generates food and a subsistence economy. This study aimed to create a model that best describes growth for *A. grunniens* and provides information on the growth of this poorly known species from the Usumacinta River. Data collection was carried out over one year through monthly sampling. A total of 447 specimens were collected from January to December 2017. Von Bertalanffy's growth constants were calculated by separate sexes using linear fit and the non-linear Levenberg-Marquardt method. Hotelling's T-squared test showed that growth was significantly faster in females than males. The estimated age at first maturity was two years in males and three in females. Considering the age reported for *A. grunniens* in other studies, the age determined in this study indicates that the population could be overexploited. Larger fish are more vulnerable to fishing pressure, mainly during their highest reproductive activity when they aggregate for spawning. More research is needed to evaluate the population status, catch per unit effort, distribution, and abundance of adults, juveniles, and larvae.
Key words: Topuche, Freshwater drum, artisanal fishery, fishing pressure.

RESUMEN. *Aplodinotus grunniens* constituye una importante pesquería artesanal en la cuenca media del río Usumacinta que genera alimento y una economía de subsistencia. La recolección de datos se realizó en un año mediante muestreos mensuales. Se recolectaron un total de 447 ejemplares de enero a diciembre de 2017. Se calcularon las constantes de crecimiento de Von Bertalanffy por sexos separados mediante ajustes lineales y el método no lineal de Levenberg-Marquardt. La prueba T-cuadrada de Hotelling mostró que el crecimiento fue significativamente más rápido en las hembras que en los machos. La edad de primera madurez estimada fue de dos años en los machos y de tres en las hembras. Teniendo en cuenta la edad reportada para *A. grunniens* en otros estudios, la edad determinada de los peces en este estudio indica que la población podría estar sobreexplotada. Los peces más grandes son más vulnerables a la presión pesquera, principalmente durante su mayor actividad reproductiva, cuando los peces se agrupan para desovar. Se necesitan más investigaciones para evaluar el estado de la población, las capturas por unidad de esfuerzo, la distribución y la abundancia de adultos, juveniles y larvas.
Palabras clave: Topuche, ronco de agua dulce, pesquería artesanal, presión por pesca.

INTRODUCTION

Sciaenidae are mainly coastal marine fish. Some of them limit their distribution to freshwater environments in the rivers of North and Central America (Chao 2002). This is the case of *Aplodinotus grunniens*, commonly known as the freshwater drum or topuche. This species is commercially important in Mexico in several regions (SAGARPA 2004, 2005, 2014, Rivera *et al.* 2015), particularly in the Usumacinta river, supporting an essential artisanal fishery. However, studies on its biology and ecology are scarce, and the few existing focus on parasites, embryonic and larval development (Hernández-Gómez *et al.* 2013), and reproductive biology (Hernández-Gómez *et al.* 2017, Hernandez-Gómez *et al.* 2019). Age studies are used to establish a fish species' growth rate and the age compositions of a given population. The otoliths are among the most reliable tools for determining a fish's age, becoming powerful instruments in fishery management (Rodríguez-Mendoza 2006). *A. grunniens* otoliths are located in the otic capsules on the cranium's ventral side, and the sagittal pair are always large. The overall shape and thickness of the sagittal otolith are characteristic of each genus, and the configuration of the tadpole impression often provides a specific identification for each species (Chao 2002). Studies of age and growth in *A. grunniens* have been conducted in the Mississippi River (Butler and Smith 1950) and Lake Erie (Bur 1984) using scales. Otoliths have been used to calculate weight and length in specimens of this species from the Mississippi River at Hannibal, Missouri (Witt 1960), as well as age in five Alabama rivers (Rypel *et al.* 2006), growth dynamics in the Winnipeg and Manitoba lakes, in Canada, and sexual dimorphism in Alabama rivers (Rypel 2007). These studies indicate that the species can live up to 42 years, and males and females differ in growth rates during adulthood, reaching 48.0 cm TL in males and 58.4 cm TL in females. In addition to representing an economic resource and food source for the rural population, *A. grunniens* plays an ecological role in controlling some mollusk populations (French 1995). The objective of this study aimed to provide information on growth and age composition through otolith sections in specimens obtained from an artisanal fishery in the state of Tabasco, Mexico. This is particularly important since growth rates and maximum ages may vary significantly between populations in North America and those in Central America, providing information to support the appropriate management of the species in the region based on those variables.

MATERIALS AND METHODS

Study area

The Usumacinta basin is an essential hydrological network located in a region with the highest precipitation in Mexico, especially in the upper portion, where the average annual rainfall can reach more than 4 500 mm (March and Castro 2010, Villela and Montero 2018). It is part of the Grijalva-Usumacinta river system, considered one of the most important basins in Mexico and North America. The Usumacinta River is the largest in Mesoamerica and among the most significant shared water resources in the Western Hemisphere. The watershed drains one of the region's largest areas of contiguous tropical forest, and it is very rich in natural resources. Because of its high river input, extensive wetlands, and the nature of the shallow shelf, this area has very high primary and fisheries productivity (Yáñez-Arancibia *et al.* 2009). The entire basin covers an area of ~110 000 km^2 and is located in Tabasco and the northeastern part of Chiapas, Mexico (March and Castro 2010) (Figure 1).

Sample collection

The collection of specimens was based on the local commercial fishery of this basin, which covers the Boca del Cerro Canyon (17° 25' 33" N, 91° 29' 29" W) to the area called El Copo (17° 57' 16" N, 91° 50' 23" W) (Figure 1). Specimens were captured from January to December 2017. During the low and mid-river levels (January-July), fish were caught with an 80 m seine net (3 m high; 20-mm mesh), while during the high levels (August- December), fishers used hook and line with crayfish *Procambarus llamasi* as bait. Each specimen was assigned a collected
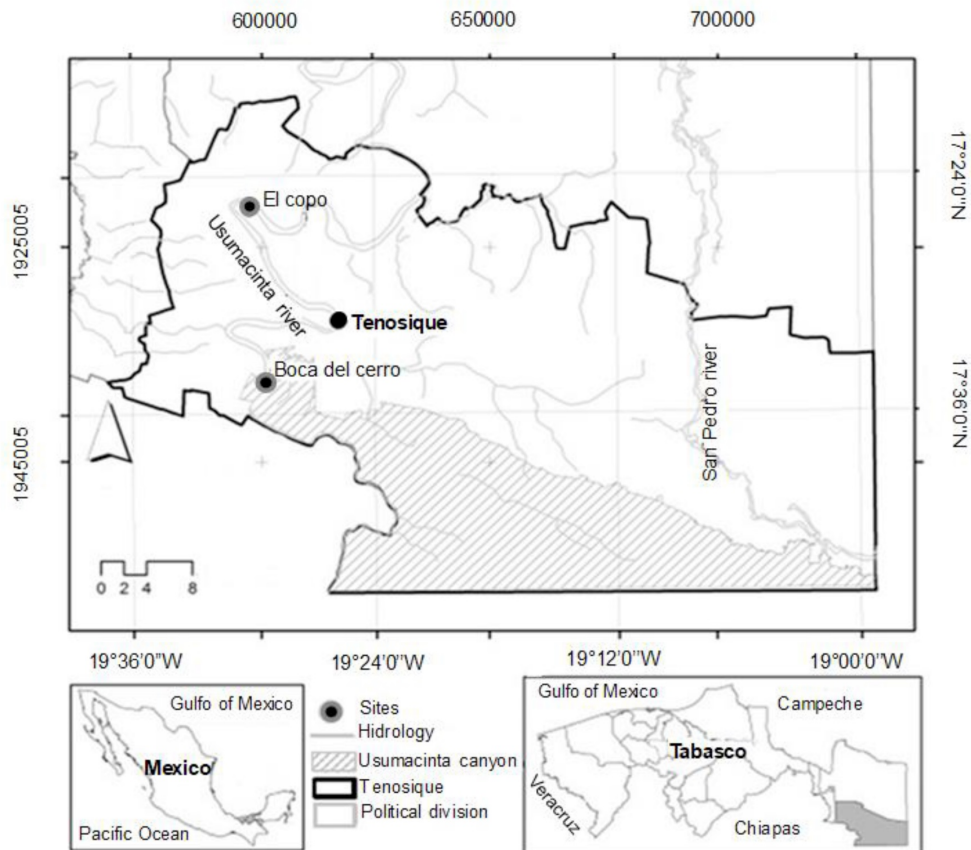
Figure 1. Map of the study site showing the sampling area in the river extending from "Boca del Cerro" to "El Copo". Tenosique indicates the location of the Fishermen's cooperative.

specimen number, and their total length (TL) and total weight (TW) were recorded to the nearest 1 mm using an ichthyometer and a digital scale (0.40 to 20 kg), respectively.

Temperature data

Data for the water temperature in the river were obtained from CONAGUA (Mexican National Water Commission) weather station number 30019, located at the Boca Del Cerro village, close to the study area.

Otolith extraction and processing

Each pair of sagittal otoliths was extracted from the inner ear's semicircular cavity through the isthmus by removing the gills and entering the cranium through the roof of the oral cavity. Each otolith was rinsed with running water, dried, and stored in ade-

quately labeled envelopes. For this research, only the right otolith was selected for data collection. The core of the otolith was marked with a pencil to initiate the cutting process. Each otolith was roasted on an electric grill until brown to highlight growth rings, put in 4.0 ml of synthetic resin, inside an approximately 3.0 cm diameter by 4.5 cm high plastic cylinder, and labeled based on the number of each specimen. When the blocks solidified, three 7 μm cross-sections were cut in each otolith, one to the left of the core, one keeping the core (central cut), and one to the right of the core. A Buehler$^\circledR$ IsoMet^{TM} 1000 Low-Speed Petrographic Cutter with a diamond blade was used to make the cuts. The sections were mounted on microscope slides with Cytoseal60 mounting medium and polished with 2 000 and 2 500 grit sandpaper to make the growth rings visible in a stereo microscope

with a transmitted light base.

Since otolith cuts did not show growth zones in detail, they were roasted again in a high-power Panasonic® microwave on microscope slides. This procedure lasted one to two hours, with intermediate breaks to monitor the roasting progress. Subsequently, two drops of pure liquid Eugenol were applied to each cut to clarify and better determine (opaque and translucent) growth rings, which indicate annual growth. Cuts were photographed with a Moticam 2300 3.0M Pixel camera, adapted to a stereoscopic microscope (Zeiss, Stemi SV6).

Age determination

Three readers were assigned to determine annual growth rings using digitized photographs. The first reader detected and counted each opaque area as a growth ring, while a second independent reader replicated and verified the assigned age. The third independent reader decided on any discrepancies in age estimates between readers 1 and 2 (Rypel *et al.* 2006).

Age of maturity

The average age of sexual maturity, defined as the age at which 50% of fish are sexually mature (A_{50}) and the age at which all individuals are fit to participate in the reproductive process (A100) actively, was obtained based on relative frequencies of individuals adjusted using King's Logistic Function. The equation modified for age is AA = $1/(1 + \exp^{-r(A-Am)})$, where: r = slope of the curve and A_m = maximum mean age, which corresponds to 0.5 (50%) proportion.

Data analysis

The total weight (*TW*) was recorded in g, total length (*TL*) in cm, and age (*A*) in years in an electronic database. Regressions were performed after logarithmic transformations to determine the TL-TW relationship of the specimens using the $TW = aTL^b$ equation, where *TW* is the somatic weight, a is the intercept (initial growth coefficient or condition factor), *TL* is total length, and b is the slope (growth coefficient) (Riker 1975). Values of the exponent b provide information on fish growth. When b = 3, the increase in weight is isometric. When the value of b is different from 3, the weight increase is allometric. When the value of b is < 3, the growth rate is considered negative allometric; when b is > 3, there is positive allometric growth (Ricker and Carter 1958). The value of b for males and females was tested using a Student's t-test (Ho: b = 3) (Sokal and Rohlf 1996). An analysis of covariance (ANCOVA) was used to determine if growth rates varied significantly between males and females (Sokal and Rohlf 1996, Zar 1999). The age frequencies of the specimens were recorded based on the readings set by the readers for each otolith. The von Bertalanffy growth model was used to estimate the length-age relationship. The model was described by the equation $L_t = L_\infty(1-e^{-k(t-to)})$, where L_t = average total length at age t, L_∞ = asymptotic total length; k = growth coefficient, and t_0 = hypothetical length at age zero. Growth parameters were estimated for combined sexes using the Ford-Walford linear method (Walford 1946) and were linearized using the von Bertalanffy growth function. This first approximation was used to calculate final growth parameters by employing a non-linear regression using the Levenberg-Marquardt algorithm method (Saila *et al.* 1988, Sparre and Venema 1997, Rico *et al.* 2001). Hotelling's T^2 test was used to compare the growth curves between males and females. This test assumes that L_∞, k, and t_0 estimates from the sex combination were obtained from a normal distribution (Bernard 1981). The monthly frequency of each sectioned otolith's margin or translucent edge was recorded to assess the formation of annual growth rings. The monthly proportion of translucent (TD) - opaque (OP) edges were compared per month using a contingency table with a Chi-square test (X^2) (Zar 1999). All statistical tests were performed using the software STATGRAPHICS CENTURION® v18.0. A p-value of <0.05 was considered to be statistically significant.

RESULTS

A total of 453 *Aplodinotus grunniens* organisms were analyzed, 245 were male, and 208 were female. The minimum and maximum total length (*TL*) were

25.03 and 42.00 cm, respectively, with an average of 30.94 $\pm$ 3.36 cm. The minimum total weight (*TW*) was 132.00 g, while the maximum *TW* was 1 094.40 g, averaging 336.00 $\pm$ 161.83 g. The TW-TL relationship analysis between females and males showed significant differences (ANCOVA: F = 6.32, P < 0.01), with females reaching larger sizes than males, and linearized curves indicated a tighter ratio in females. The general equations for the *TW-TL* relationship were $TW = 0.0007 (TL)^{3.7974}$ (r^2-0.90) for females and $TW = 0.0180 (TL)^{2.8812}$ ($r^2 = 0.71$) for males (Table 1). Student t-test results found that the b value from the weight and length relationship in females was positively allometric (b > 3; p < 0.05), while in males was negatively allometric (b < 3; p < 0.05).

Table 1. Average total length in cm (mean $\pm$ SD) for the age of *Aplodinotus grunniens* caught in the middle basin of the Usumacinta River, Tabasco, Mexico.

Age	Females	Males
2	28.63 $\pm$ 1.12	27.82 $\pm$ 1.30
3	32.67 $\pm$ 2.17	30.02 $\pm$ 1.28
4	36.14 $\pm$ 1.94	32.09 $\pm$ 1.82
5	37.65 $\pm$ 1.70	32.57 $\pm$ 1.55
6	36.83 $\pm$ 1.47	-
7	42.00	32.20
8	42.00	32.00

The studied population comprised seven age groups; the minimum age was two years, and the maximum was eight years (Figure 2, Figure 3). For both sexes, ages 2 and 3 represented the maximum frequencies (37.16 and 38.93%, respectively), while ages 7 and 8 represented the minimum frequencies. Each age group had *A. grunniens* males and females recorded, except for males in age group 6 (Table 2). No specimens from age groups 0 and 1 were observed. The average error rate recorded from the three age readers was 7.86%, with an 8.34% coefficient of variation.

The analysis of otolith margins indicated no differences in the monthly ratio of the otolith growth margins (X^2 = 6.87, df = 9; P < 0.05). Slight patterns showing a larger proportion of translucent edges were observed between April and May, the months with higher temperatures (average temperature 27.66 $\pm$ 1.15 ℃), and again in December, just at the end of the spawning season with a proportion more significant than 50% (Figure 4). The number of individuals with opaque and translucent otolith margins slightly varied around 50% during the reproductive season. No seasonal or annual growth pattern was statistically detected when relating the water's surface temperature with the marginal formation of the otolith rings of *A. grunniens*. In addition, it was also observed that opaque edges were more prompt to be formed at low temperatures during January (25.52 $\pm$ 1.51 ℃), March (24.31 $\pm$ 1.33 ℃), and November (26.4 $\pm$ 1.6 ℃). Otolith edges from July and October were not considered in the statistical analysis because the organisms collected were scarce (n = 1 and n = 2, respectively); this represented a variability in the readings that could have produced an incorrect data association.

The estimates obtained from the von Bertalanffy growth model were TL_∞ = 41.15(l-a$^{0.2824(t-2.0779)}$) for both sexes, TL_∞ = 42.45(l-a$^{0.3575(t-1.1341)}$) for females, and TL_∞ = 34.01(l-a$^{0.4918(t-1.4457)}$) for males (Figure 5). Showing significant differences between males and females (T^2_{obs} = 23861.40 > T2 = 11.52, P < 0.001).

A. grunniens males and females reach sexual maturity (A_{50}) at ages 2 and 3 years, respectively, and all specimens are sexually mature (A_{100}) at ages 5 and 6 years, respectively (Figure 6).

DISCUSSION

Sexual dimorphism in *A. grunniens* is evidenced by the total length (TL) and total weight (TW) relationship. In this study, females showed greater growth rates than males; as confirmed by Von Bertalanffy´s model, females were significantly larger and had relatively lower growth rates than males. This trait has been reported for *A. grunniens* in the Wabash River, where the genders also show different growth patterns (Jacquemin *et al.* 2015). In contrast, Bur (1984) found no differences between sexes in specimens studied in Lake Erie. Other species of the Sciaenidae family inhabiting marine environments do not show sexual dimorphism; this
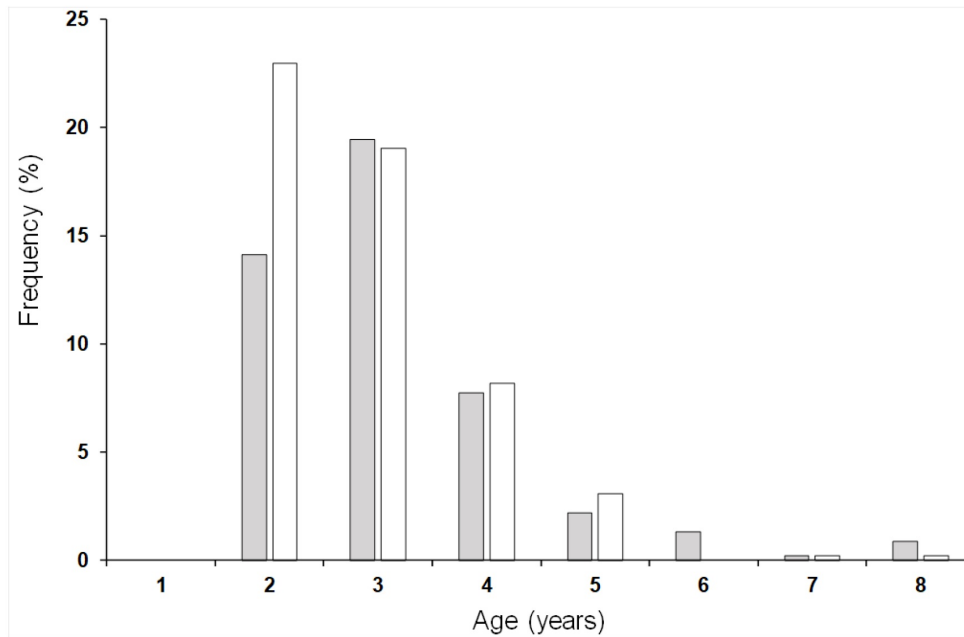
Figure 2. Frequency of age (years) of *Aplodinotus grunniens* caught in the middle basin of the Usumacinta River, Tabasco, Mexico: females (shaded bars) and males (white bars).

is the case for *Micropogonias furnieri*, *Sciaena umbra*, and *Argyrosomus japonicus* (Griffiths and Hecht 1995, La Mesa *et al.* 2008, Borthagaray *et al.* 2011). Our study suggests that *A. grunniens* growth patterns differences lead to larger females producing more oocytes and having higher energy reserves in the form of fat to produce and form follicular cells (Parker 1992). However, Rypel (2007) speculated that sexual dimorphism in *A. grunniens* could also be related to migration patterns, applying the concept of "partial migration of niches". He considered that females are often more motile than males; therefore, being larger confers higher survival probabilities. Rypel (2007) mentioned that the reasons some fish move are not well understood; however, if the females move to avoid stressors (limited food resources, competition, or severe environmental conditions), their goal could be to reach an optimal reproductive state (Shreck 2010). Regarding alternative reproductive tactics, Brockmann and Taborsky (2008) highlighted the different alternative reproductive tactics that species occupy to achieve reproduction, including sexual dimorphism and partial migration.

    A. grunniens is the only freshwater species

of the Sciaenidae family in the Americas (Chao 2002, Sluss and Harrel 2006). It is a widely distributed species covering the great lakes in Canada to southern Guatemala, and significant differences have been reported between sites. In terms of age structure, we found that the population in the study area, as determined using the otoliths, reflects a relatively young population since the oldest fish captured were eight years old. Similar results were observed in the Tensaw and Missouri rivers and in the Lake Claiborneque, where fish had similar age groups as those found in this study (Rypel *et al.* 2006, Rypel 2007, Shields and Beckman 2015). In contrast, in the Wabash River and other water bodies in Alabama, the older ages reported vary between 22 and 32 years, respectively (Jacquemin *et al.* 2015). Interestingly, data reported by Rypel (2007) indicate that ages vary greatly between rivers, creeks, and lakes in Alabama, USA. In the Alabama River, the oldest fish was five years old (n = 23), while in the Cahaba River, the fish reached up to 32 years (n = 34). In the same study, the oldest fishes found in the Clairborne Lake (n = 23) and the Tensaw River (n = 12) were nine years old. These variations in age could be related to the sam-
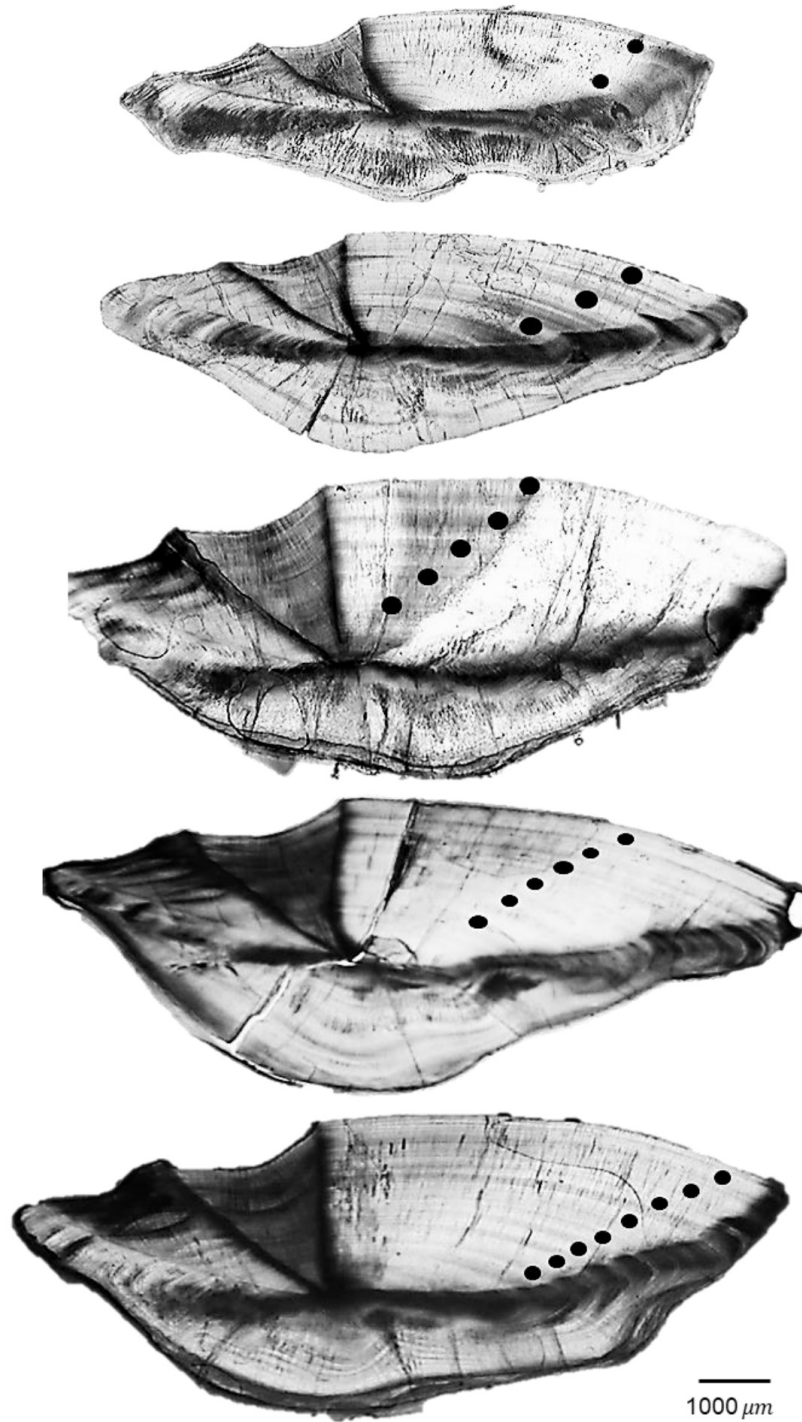
Figure 3. Cross-section of (sagittal) otoliths showing the ages of *Aplodinotus grunniens* captured in the Usumacinta River, Tabasco, Mexico.

Table 2. Age-length distribution in males and females of *Aplodinotus grunniens* obtained by otolith count.

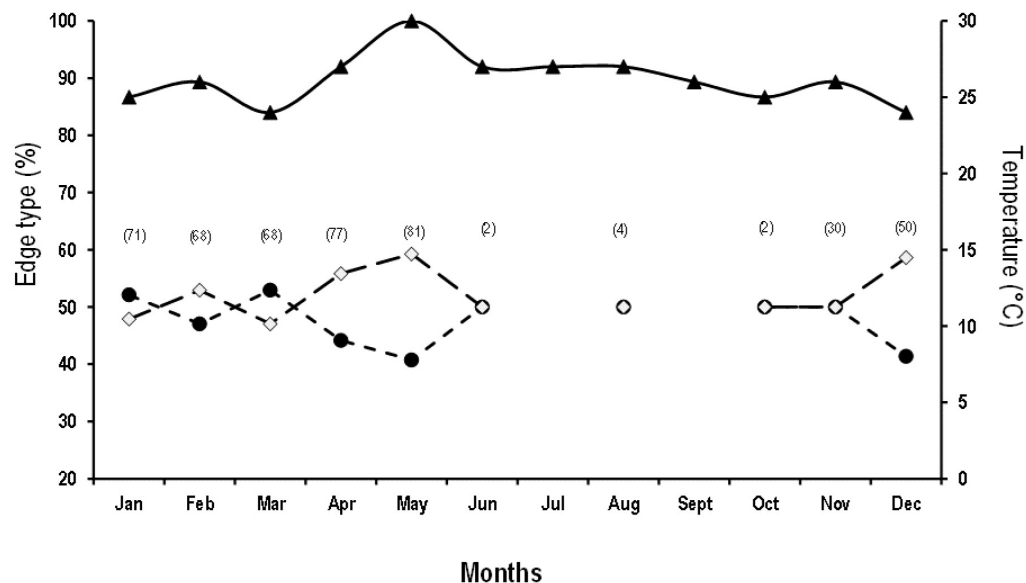| Total length (cm)	Age-class							
	1	2	3	4	5	6	7	8
Females								
25.0-26.9		2						
27.0-28.9	26							
29.0-30.9	34	14						
31.0-32.9	2	34	1					
33.0-34.9		24	6					
35.0-36.9		11	15	4	2			
37.0-38.9		5	9	3	4			
39.0-40.9			3	3				
41.0-42.9			1			1	4	
Males								
25.0-26.9	20							
27.0-28.9	52	10						
29.0-30.9	30	54	11					
31.0-32.9	2	20	12	9		1	1	
33.0-34.9		4	10	2				
35.0-36.9			4	3				
37.0-38.9								
41.0-42.9								

Figure 4. Monthly margin ratio of opaque (open circles) and translucent (filled circles) growth rings of *Aplodinotus grunniens* in relation to the temperature of the Usumacinta River (filled triangle), Tabasco, Mexico. The number of fish per month (n) is shown in parentheses.

ple size, sampling biases, food availability, and flow velocity, among other factors (Rypel *et al.* 2006). Since we used the same methodology reported by Rypel *et al.* (2006), Rypel (2007), we are confident that there is no underestimation of age; however, we do not discard that the factors mentioned above may

drive the estimated ages obtained in this study.

Age variations observed may be influenced by habitat and environmental conditions (Rábago-Quiroz 2011), as well as by predation, diet, food availability, fishing activity in the area (pressure for fishing prevailing in the area), and fisheries resource
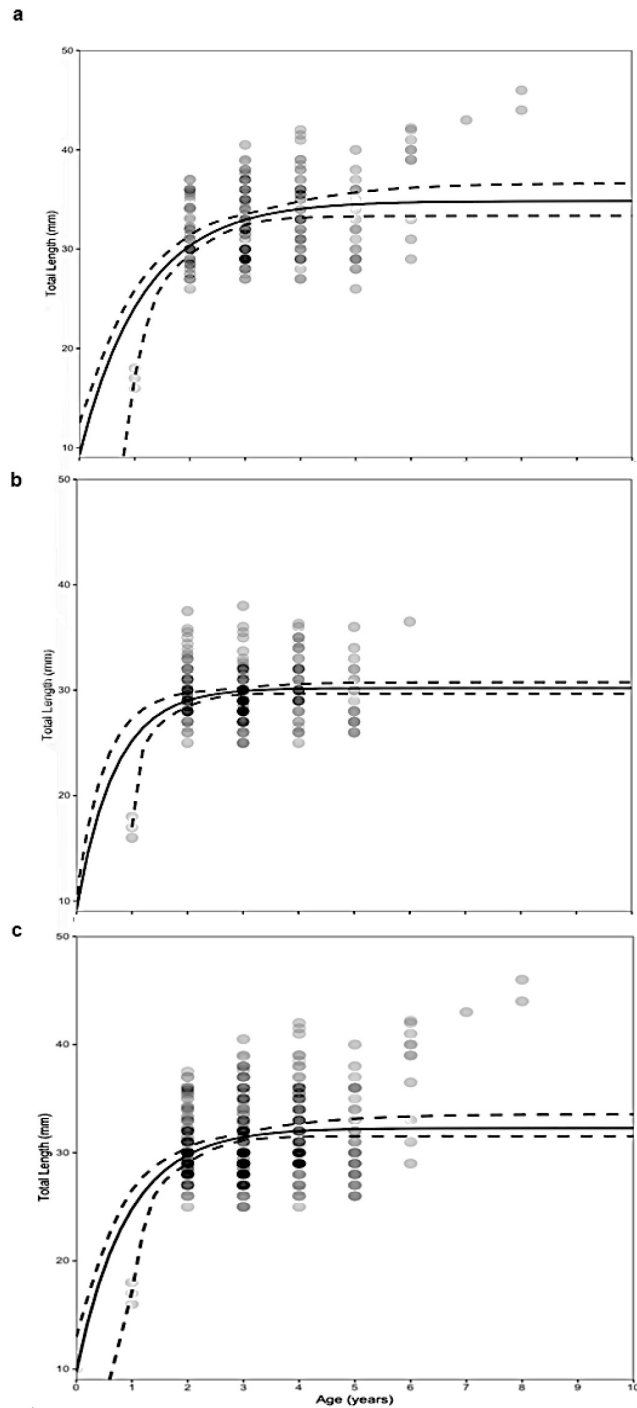
Figure 5. Von Bertalanffy growth curves of *A. grunniens* for females (a), males (b), and both sexes (c) in the middle basin of the Usumacinta River, Tabasco, Mexico. The number of fish included in the model (n) is 245 for males, 208 for females, and 453 in total.
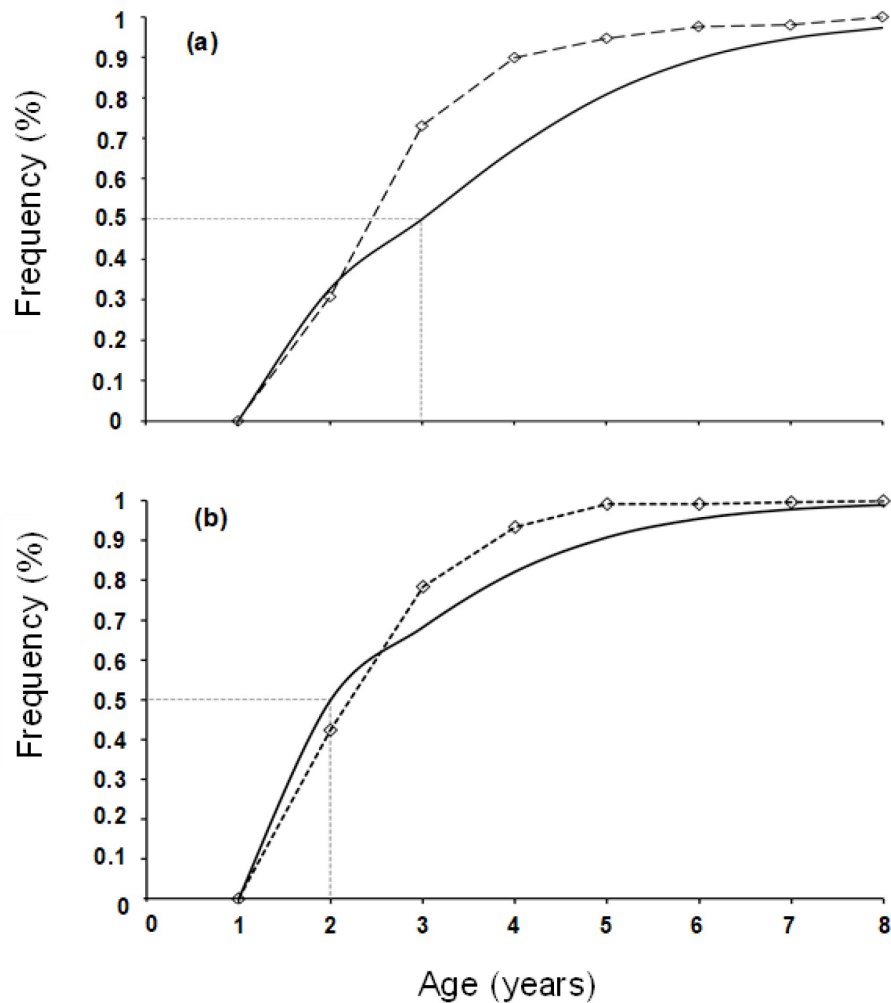
Figure 6. Frequency of age of first sexual maturity (A50) of *A. grunniens* captured in the middle basin of the Usumacinta River, Tabasco, Mexico. Females (a) and Males (b). Value observed (dotted line) and Adjusted (continuous black line).

management (sizes allowed to catch). In the study site, the fishing pressure on larger fish might be the main reason since larger fish are the fishers' target. This could result in the selective harvest of large females, eliminating valuable breeders from the population.

Aging fish using otoliths is considered the method with the highest precision. Several studies have mentioned that this technique is better than scales, recommending that precision should rely on the agreement between readers (Hoxmeier *et al.*

2001). In our study, using three readers provides enough confidence to age the fish; unfortunately, this method requires killing the fish.

This study's most frequent age groups were those of two years with average sizes of 28.22 $\pm$ 0.58 cm TL and three years with average lengths of 31.34 $\pm$ 1.87 cm TL, which coincides with the species recorded in the Missouri River (Shields and Beckman 2015). However, these ages differed from the frequencies recorded for the Louisiana populations with specimens under four years (8.67%) and the pro-

portion of the Alabama fish for the age of 3 years (14.00%). It is important to consider that the fish sampled in this study come from the local fishery, and the peak captures coincide with reproductive events; therefore, these results reflect that young adults actively participate in the reproduction events, becoming part of the fish recruitment when they enter the fishing area, during months of higher reproductive activity, January-June and October-December (Hernández-Gómez *et al*. 2017).

Ages one year and under were not documented in this study, probably because of the type of fishing gear used or the dependence on fishery samples in the area. However, young fish (one year and under) may occupy a different niche in the river system since the eggs of this species are pelagic; therefore, they are transported by the current downriver. The dynamic interaction between food availability and predation in juvenile fish probably causes changes in the habitat of the species and the nocturnal use of coastal habitats. Consequently, it is assumed that *A. grunniens* specimens (0 to 1 year) in the middle basin of the Usumacinta River remain in areas close to the coast where there is greater availability and abundance of food and shelter.

No statistical growth patterns were observed in this study, as revealed by analyzing otolith edges or monthly otolith increases. In this study, slight patterns are associated with higher temperatures and the end of the reproductive season, but, due to the lack of a strong sample size during some months, more information is needed to elucidate the growth patterns of *A. grunniens* in the Usumacinta River. The cause of ring formation has been biologically related to temperature because changes in this environmental factor accelerate or delay the speed of biochemical reactions (Tarifeño 2004, Hernández-Gómez *et al*. 2017). Consequently, the net effect of ambient temperature change on the physiology of *A. grunniens* may depend on the temperature divergence and the range and speed at which the change occurs, as Tarifeño (2004) mentioned. Little *et al*. (2020) indicated that energetics are particularly relevant for growth and movement; therefore, plastic responses to thermal signals mean that fishes can modulate their acute

thermal responses to compensate at least partially for thermodynamic effects, and temperature can have pronounced effects on energy metabolism (Little *et al*. 2020). In *Micropogonias furnieri*, growth is reflected as a consequence of a combination of factors: the decrease and low water temperatures in winter, the beginning of gonadal development, and a food supply to the end of the reproductive season (Borthagaray *et al*. 2011). The deposition periodicity of growth increments in *Sciaena umbra* shows an annual pattern. It also proved that the opaque zone was deposited between March and June (Chater *et al*. 2018); the authors suggest that the formation of alternating translucent and opaque zones could be related to a complex control by environmental and endogenous factors, indicating that physiological changes are produced mainly by cyclic variations of temperature, photoperiodism, and food supply.

In the Usumacinta River, the highest temperatures occur from April to August, coinciding with a slightly higher proportion of fish showing translucent otolith margins, indicating faster growth. On the other hand, minimum values of temperature variability were recorded between June and November. Half of the fish had translucent otolith edges during this period, and the other half had opaque edges. This pattern could be related to the metabolic activity required by gonadal development and spawning, indicating that the opaque otolith reflects females' most significant energetic demand. Therefore, during those months, a significant amount of energy is focused on gonadal development, maturation, and spawning. Similar patterns have been reported in *Argyrosomus inodorus*, where the wide opaque zone was formed from August to February, coinciding with the primary spawning season (Griffiths 1996). In *Centropomus undecimalis*, the translucent band was deposited mainly during the summer, coinciding with high temperatures and food abundance. In contrast, the opaque band formed each winter has been attributed to slow growth associated with low temperatures, gonadal maturation, and spawning (Perera-Garcia *et al*. 2013).

A previous study in the Usumacinta River documented that the reproductive phase in *A.*

grunniens tends to be extended, but a distinctive peak occurs from June to November (Hernández-Gómez *et al.* 2017).

Based on the VB growth equation and the statistical comparisons used in this study, females were significantly larger and showed relatively lower growth rates than males. In both sexes, the growth curve has a relatively constant slope with a low k value; consequently, *A. grunniens* in the Usumacinta River takes time to reach the asymptotic limit. The growth of this species on the Usumacinta River differs from the one recorded in the Alabama River and Lake Erie for females (L_∞ = 52.03cm) but is similar to that one of males (L_∞ = 38.53cm) (Bur 1984, Rypel 2007). This difference is also present in the growth of the species captured in lentic and lotic reservoirs in Alabama (L_∞ = 61.56cm and $L_{a\infty}$ = 45.48cm, respectively) (Rypel *et al.* 2006). In contrast, *Argyrosomus inodorus* and *Otolithes ruber* - marine species of the same Sciaenidae family-differ from *A. grunniens* showed the same growth pattern in both sexes, indicating no sexual dimorphism (Griffiths 1996, Brash and Fennessy 2005).

The L_∞ reported in this paper for *A. grunniens* is consistent with the one obtained in the Alabama and Mississippi rivers, where L_∞ = 35.2cm for males, but differs from that one for females (L_∞ = 39.5cm and L_∞ = 60.3cm, respectively) (Richard and Rypel 2013). They were also similar to the organisms analyzed in the Wabash River (females: L_∞ = 41.3 $\pm$ 2.66 cm; males: L_∞ = 35.6 $\pm$ 2.11 cm) (Jacquemin *et al.* 2015). Therefore, it can be inferred that *A. grunniens* growth responds to spatial and temporal habitat variations, which may be inconsistent, as seen in the Illinois River for this same species (Smith *et al.* 2007).

Aplodinotus grunniens has been described as a warm-water eurythermic fish, possessing enzymatic limitations which dictate that growth occurs only when the water temperature is above 10 °C. Below this temperature, metabolism slows, and the fish remain relatively inactive, no longer growing (Patterson 1998, Braaten and Guy 2002). Although a hardy species, the freshwater drum from North America show difficulty in coping with water temperature exceeding 25.6 °C (Becker 1983); in Lake

Erie, freshwater drums collected throughout the central basin (between 3 and 24 m depth) in spring, yearling and older freshwater drums were most abundant in bottom strata when water temperatures were 3.4 ° to 13.1 °C. In contrast, abundance in bottom strata declined in summer when water temperatures rose as high as 19.8 °C (Bur 1984). A very different situation might be observed in tropical areas since, during the present study, the average temperature ranged from 24.31 °C to 27.66 °C, suggesting an adaptive response to high temperatures in the region.

The age at first sexual maturity in *A. grunniens* was estimated at two years for males (27.7 cm) and three years for females (33.1 cm), indicating that the species initiate reproduction early in their life, at small sizes. A higher abundance of sexually mature fish was observed in five-year-old males and six-year-old females. These records are similar to those reported for both sexes in the Mississippi River and Lake Erie but differ in the age of maturity for females (Becker 1983). Similar ages were reported for specimens caught in Lake Winnebago, where males usually mature at ages 3-4 years and females at 4-5 years (Becker 1983, Bur 1984). Something similar was reported for Lake Erie, where males mature at ages 2-5 and females at 4-6 years old (Becker 1983). However, Daiber (1953) indicated that those fish in northern regions differ in size when reaching the age of sexual maturation (20.3 cm and 22.1 cm TL, respectively). Compared to the organisms in Lake Winnebago, males and females varied in maturity size (2 years, 22.6 cm TL and five years, 27.2 cm, respectively) (Davis-Foust *et al.* 2009). Even though age and size at first maturity are inheritable traits, the change to lower ages and sizes is a function of genotype frequency in the population over time (Saborido-Rey 2006). The pressure of overexploited stocks can push fish populations to grow faster and mature at younger ages, displaying associated changes in size at maturation (Sharpe and Hendry 2009).

The oldest age recorded in *A. grunniens* in the Usumacinta River (8 years) was lower than in other populations, such as the one recorded in the Missouri River by Shields and Beckman (2015), where the collected specimens that were up to 13 years old.

The fish from our study also differs from the age of specimens recorded in the Wabash and Alabama Rivers (32 years) (Rypel 2007, Jacquemin *et al*. 2015). This difference could be due to the influence of commercial fishing on the middle basin of the Usumacinta River, where larger fish are preferred. In addition, this river's specimens grow relatively slowly, which could have influenced these records.

CONCLUSIONS

The *A. grunniens* fishery in the middle basin of the Usumacinta River is mainly supported by young, sexually mature specimens aged two to eight years old but composed mainly of ages two and three years. The reported oldest fish was eight, indicating a relatively young population. It is assumed that this situation could affect the species' reproductive cycle, mainly because females are larger and, therefore, they are potentially the most targeted size fish.

Because of size differences, the fishing pressure on females could be more significant than that on males, which reemphasizes the need to take sexual dimorphism into account in stock assessments for sexually dimorphic species; for instance, the use of sex-specific parameters related to population processes such as growth and natural mortality could be included. Research on catch per unit effort, distribution, and abundance of larvae and juveniles is urgent for this species. These measures are proposed as a precautionary mechanism to avoid undesirable situations, such as the fishery's collapse or the disappearance of the species from the region.

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