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***Research Article***

# Estimation of differential growth of the protandrous hermaphrodite marine gastropod *Trochita trochiformis* (Littorinimorpha: Calyptraeidae) using Schnute model cases

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**ABSTRACT.** The snail *Trochita trochiformis* is a mollusk captured on the coasts of Jalisco and Guerrero of the Mexican Pacific. Despite its importance in artisanal fisheries, information on its population parameters is still being determined. This research aimed to determine the diameter-weight relationship, sex ratio, cohorts, and growth of this species. Specimens were captured from October 2019 to September 2021. Shell diameter ($S_d$), total weight ($T_w$), and the sex of the organisms were gathered from a total of 1763 females and 956 males. The sex ratio was 1.84:1, and the $X^2$ test ($P < 0.05$) indicated significant differences. The $S_d$-$T_w$ relationship for females and males was potential-type. The values of the allometry coefficient for both sexes were $b = 2.61$, $b = 2.60$ for females, and $b = 2.62$ for males. In all three cases, the t-Student test indicated negative allometric growth, which indicates that the species first grows in shell diameter, then in body weight. The ANCOVA did not show significant differences in the $S_d$-$T_w$ relationships between sexes ($P = 0.902$). The Kolmogorov-Smirnov test applied to the $S_d$ data showed differences between sexes ($P < 0.001$). In females, differences were observed in 71.5% by monthly comparisons, while in males, differences were found in 58.1%. Multinomial analysis showed three modal groups and 14 individual cohorts for both females and males. Case 2 of the Schnute model was the best for females (*wi* = 0.39) and males (*wi* = 0.53), showing sigmoidal Gompertz-type growth. The resulting growth curves showed that females exhibit accelerated growth concerning males and that both sexes reach their maximum size, 88.04 and 86.23 mm, respectively, at approximately 10 years of age.

**Keywords:** *Trochita trochiformis*; protandrous hermaphrodite; recruitment; multimodel analysis; Schnute model

## INTRODUCTION

Coastal fishing is one of the most productive activities in coastal areas. Populations settled near the coasts to obtain economic and nutritional benefits from extracting natural resources (Gutiérrez-Zavala & Cabrera-Mancilla 2012). Among these resources, mollusks constitute an alternative to popular food. It is essential to intensify the fishing studies on these resources to achieve their maximum use through rational use to be able to preserve the sustainability and health of the environment and the ecosystem, which should have an impact on the supply and sources of employment for fishers (Cavero-Cerrato & Rodríguez-Pinto 2008, García-Delgado & Leones-Zambrano 2016).

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The mollusk *Trochita trochiformis* (Born, 1778) is a protandrous hermaphrodite mesogastropod (Bolvarán 1981) of the family Calyptraeidae. It is a widely distributed species, reported from Mazatlan, Mexico, to Valparaiso, Chile (Keen 1971). The presence of *Trochita* spp. is usually related to upwelling systems (Taylor & Smyte 1985). Regarding *T. trochiformis* in Guerrero State, Mexico, it is difficult to demonstrate the presence of an upwelling area due to the lack of oceanographical studies and information in the study area. However, Taylor & Smyte (1985) mentioned that *Trochita spirata* (synonymous with *T. trochiformis*) occurs in western Mexico due to the influence of the southern end of the California upwelling system and a smaller seasonal upwelling in the Gulf of Tehuantepec.

The species is of commercial interest in the Mexican Pacific, specifically for the coasts of Jalisco and Guerrero (Ríos-Jara et al. 2004). In Guerrero State, *T. trochiformis* is caught throughout the year. Nine cooperative societies of fishing production are dedicated to extracting this species in the Costa Grande region of Guerrero, with a reported catch of about 80,000 dozen per year (Cerros-Cornelio et al. 2021). Due to the size and weight of this species on the coasts of Chile, it was commercially exploited by the artisanal fishing sector, with a reported catch of more than 2000 t between 1985-1990 (Cañete & Ambler 1992). Over the years, catches gradually decreased, and fishing increased, reporting 12 t in 2018-2019 and 27 t for 2020 (SERNAPESCA 2021). This fishery is a typical example of boom-and-bust artisanal benthic fisheries (Cañete & Ambler 1992).

Species of the genus *Crepidula* have been studied, generating much information about the biological aspects of the same family (Hendler & Franz 1971, Collin 1995, Zelaya et al. 2012). Despite the importance of *T. trochiformis* in the artisanal fisheries of the Guerrero coast, the information available on its reproductive biology and population parameters is scarce. Most studies have been carried out on the Chilean coasts and are directed to biological features such as fecundity, reproductive behavior, sexual inversion, and gonad development (Bolvarán 1981, Brown 1989, Cañete 1990, Cañete & Ambler 1992). In Mexico, Ríos-Jara et al. (2004) determined the growth of *Calyptraea spirata* (Forbes, 1852) (synonymy of *T. trochiformis*) by mark-recapture on the coasts of Jalisco.

Increasing the information on *T. trochiformis* is essential for evaluating population conditions to improve resource management practices. Because this fishery exhibits typical boom and bust dynamics (Cañete & Ambler 1992), and because of their larger size, females are more susceptible to fishing. Thus, it is necessary to understand population turnover, abundance, and how reproductive biology increases the risk of rapid overexploitation. For this reason, population and fisheries studies are necessary to provide useful information on population structure, which allows predictions on features such as recruitment, sex ratio, growth, mortality, and size at maturity, among others; this information is very important and necessary for fisheries management and for the establishment of closed seasons, catch quotas, and minimum catch sizes (Arsenault & Himmelman 1998, Villalejo-Fuerte et al. 2003, Derbali et al. 2009, García-Delgado & Leones-Zambrano 2016).

In addition, studying individual growth in organisms subject to commercial exploitation is important as it provides information on the age structure of individuals within the stock (Montgomery et al. 2010). Due to the above, this study aimed to determine population parameters, such as diameter-weight relationship, sex ratio, cohorts, and individual growth by multimodel inference, for females and males of *T. trochiformis* in the Mexican Pacific.

## MATERIALS AND METHODS

### Study area

Sampling was conducted monthly from October 2019 to September 2021 (except April 2020) at the locality of Puerto Vicente Guerrero, located in the southwestern region of the Pacific Ocean, in the Guerrero State, México (17°27'30"N, 101°03'26"W). An average of 118 specimens per month were analyzed. The organisms were purchased from fishers (fishery-dependent sampling) who work at the Costa Grande de Guerrero fishing cooperative and are dedicated exclusively to the extraction of *T. trochiformis*. The sampled organisms were extracted from the intertidal zone during low tide hours. The species were identified following Keen (1971) and Simone (2002) and considering the World Register of Marine Species (WoRMS). Specimens were measured for shell diameter ($S_d$) with a digital vernier caliper accurate to 0.01 mm. The total weight ($T_w$) was recorded using a digital balance accurate to 0.01 g. The sex of organisms was determined by direct observation: the presence of a penis structure was an indication of the males, while the presence of an ovigerous groove structure was an indication of females.

### Data analysis

The shell diameter total weight relationship was estimated for males and females by fitting the potential model through the following equation $T_w = a \times {S_d}^b$, where $T_w$ is the total weight (g), $S_d$ the shell diameter (mm), $a$ the intercept (condition factor) and $b$ the allometry coefficient. Prior to analysis, the paired $S_d/T_w$ data were transformed to the natural logarithm ($ln$) to identify out-of-range data and exclude them from the analysis. The coefficient of determination $R^2$ was used to measure goodness-of-fit for each regression. The 95% confidence intervals of the curve with 5000 interactions were estimated using Grapher™ software (Golden Software, LLC). The 95% confidence interval for $b$ was also estimated, and a t-Student test (Zar 2014) was performed to determine if isometric growth exists (Ho: $b$ = 3, $\alpha$ = 0.05). Significant differences between sexes in the relationships of the $S_d/T_w$ variables were evaluated with a one-way analysis of covariance (ANCOVA) once the assumptions of homoscedasticity of the slopes (parallelism) were found with the data transformed to the logarithm (Zar 2014). The IBM-SPSS Statistics 25 statistical package was used for this analysis.

The sex ratio (F:M) was determined through Pearson's chi-square goodness-of-fit test ($x^2$) with correction for Yates continuity (Zar 2010) and was determined if the sex ratio F:M differed from 1:1 parity.

The length ranges for each sex were estimated in a monthly fashion using box and whisker plots, and the mean, minimum, and maximum lengths were plotted for each month. Differences in the $S_d$ distribution between months were determined using the Kolmogorov-Smirnov two-sample goodness-of-fit test (Gotelli & Ellison 2004) using the IBM-SPSS Statistics 25 statistical package.

The size structure was determined monthly. The data were grouped into 4-mm intervals, and a multinomial analysis was performed to identify modal groups. This analysis is based on the observed distribution using frequency histograms, and the estimate of each modal group ($a$) was calculated using a normal probabilistic density function (multinomial analysis) according to the following (Haddon 2011):

$$F_i = \sum_{a=1}^{n} \left[ \left( \frac{1}{\sigma a \sqrt{2\pi}} \right) e^{\frac{(xi-\mu a)^2}{2\sigma a^2}} \right] \times P_a$$

where: $F_i$ is the expected frequency of the length interval $i$ for the whole sample, $xi$ is the midpoint of the length interval $i$, $\mu a$ the mean length of group $a$, and $P_a$ is the weight factor of cohort $a$. The analysis was then fitted with the maximum likelihood method using the Microsoft Excel Solver™ add-on (Hilborn & Mangel 1997):

$$LL\{\hat{\mu}_a, \sigma_a^2, \lambda_a\} = -\sum\nolimits_{i=1}^{n} f_i Ln\left(\frac{F_i}{\sum F_i}\right) \times [\Sigma f_i - \Sigma F_i]^2$$

where: $LL\{\hat{\mu}_a, \sigma_a^2, \lambda_a\}$ is the probability value of the parameters; $\hat{\mu}_a, \sigma_a^2$ y $\lambda_a$, $f_i$ the total observed frequency of diameter group $i$, and $F_i$ the total expected frequency of diameter group $i$ according to the multinomial model (Montgomery et al. 2010, Haddon 2011). Finally, the modal groups of *T. trochiformis* were separated according to two criteria: the first criterion was the separation index ($SI$) using the following equation (Sparre & Venema 1998):

$$SI = 2 \times \frac{(\mu_2 - \mu_1)}{(\sigma_1 + \sigma_2)}$$

where: $\mu_n$ and $\mu_i$ are the $S_d$ average of modal groups $n$ and $i$, respectively; $\sigma_n$ and $\sigma_i$ are the standard deviations of modal groups $n$ and $i$, respectively. Therefore, if $SI > 2$, it is feasible to separate the normal components from the observed frequencies (Sparre & Venema 1998).

The second criterion was the Akaike information criterion ($AIC$) (Burnham & Anderson 2002). The smallest value of the Akaike's bias correction ($AIC_c$) was used to select the best statistical fit of the size group number using the following equation (Ortega-Lizárraga et al. 2016):

$$AIC_c = 2\,(k - LL) + \left( \frac{2k(k+1)}{n-k-1} \right)$$

where: $k$ is the total number of parameters of the cohorts, $LL$ is the logarithmic maximum likelihood function, and $n$ is the number of observations.

The mean lengths for each identified modal group were plotted on a time scale. The probable number of cohorts supporting growth was obtained by modal progression through time in an ordered sequence (Montgomery et al. 2010), allowing a visual comparison over time, and it was possible to generate alternative hypotheses about the exact modal progression (Avila-Poveda et al. 2020).

For all modal progressions found, the length increment data ($S_d$) versus time increment $\Delta_t$ were obtained as equivalent representations of the mark-recapture data (Baker et al. 1991). These data were used to estimate individual growth parameters, using the five cases of the Schnute model (1981), which allow comparisons between growth curves, providing both asymptotic and non-asymptotic growth; one of these (case 5), is a special case based on the von Bertalanffy growth function (VBGF), which was described by Baker et al. (1991) and was derived from Schnute growth models (1981). Baker's derivatives are equivalent to circumstances in which direct information on length at a specific age is not available (Baker et al. 1991, Quinn & Deriso 1999). The five cases are as follows:

Case 1 (assuming $a \neq 0$ and $b \neq 0$) is given by

$$Y_2 = \left[Y_1^b * \exp^{-a\Delta t} \times \varepsilon^b\left(1 - \exp^{-a\Delta t}\right)\right]^{1/b}$$

Case 2 (assuming $a \neq 0$ and $b = 0$) is given by

$$Y_2 = \exp[\text{Ln}\,(Y_1) \times \exp^{-a\Delta t} \times \text{Ln}(\varepsilon)(1 - \exp^{-a\Delta t}]$$

Case 3 (assuming $a = 0$ and $b \neq 0$) is given by

$$Y_2 = \left(Y_1^b + \varepsilon^b\, \Delta_t\right)^{\frac{1}{b}}$$

Case 4 (assuming $a = 0$ and $b = 0$) is given by

$$Y_2 = Y_1 \times \varepsilon^{\Delta t}$$

Case 5 (assuming $a > 0$ and $b = 1$) is given by

$$Y_2 = \left[Y_1 \times \exp^{-a\Delta t} + \varepsilon\left(1 - \exp^{-a\Delta t}\right)\right]$$

In all five cases, $Y_1$ and $Y_2$ are mean lengths for the same cohort at collection times $t_1$ and $t_2$; $a$ is the growth parameter; $b$ is related to the inflection point within the growth curve; $\Delta_t$ is the elapsed time between $t_1$ and $t_2$, and $\varepsilon$ is the asymptotic length or maximum theoretical length ($L_\infty$), equivalent to the von Bertalanffy growth model for cases 1, 2 and 5.

For the Schnute model cases, the data were fitted using the log maximum likelihood function $LL$ (Haddon 2011), considering additive error with the following equation:

$$LL\,(\Phi|\text{data}) = \left(-\frac{n}{2}\right) \times [ln\,(2\pi) + 2\, \times ln\,(\sigma) + 1],$$

where: $\Phi$ represents the model parameters, $n$ the number of observations, and $\sigma$ the standard deviation calculated by additive error. The formula for the standard deviation is as follows:

$$\sigma = \sqrt{\frac{\sum\sqrt{\left(S_{d_{\text{obs}}} - S_{d_{\text{cal}}}\right)^2}}{n}}$$

where: $S_{d_{obs}}$ is the observed shell diameter, $S_{d_{cal}}$ is the calculated shell diameter, and $n$ is the number of observed $S_d$ data.

For comparisons of the Schnute model cases and selection of the best model describing $S_d$ as a function of time, Akaike corrected form ($AIC_c$) scores were used (see above). The lowest $AIC_c$ score is the one that will define the best model (Burnham & Anderson 2002, Katsanevakis 2006, Katsanevakis & Maravelias 2008).

The difference ($\Delta_i$) in the $AIC_c$ of a given model concerning the $AIC_{min}$ of the best model was estimated with the following equation $\Delta_i = AIC_c - AIC_{min}$. This analysis yields three possible answers for selecting the best growth model. In the first case, if $\Delta_i > 10$, the candidate growth model should be discarded since it does not describe the observed growth and is not supported by the data. In the second case, if $4 < \Delta_i < 7$, the model partially supports and weakly explains the growth data. Finally, in the third case, if $\Delta_i < 2$, the candidate growth model adequately describes the observed growth data (Burham & Ardenson 2002, Avila-Poveda et al. 2020).

Normalized weights for each growth model (Akaike 1983, Burnham & Anderson 2002) were estimated using the Akaike weight ($wi$), expressed as a proportional index defined as:

$$wi = \frac{e^{(-0.5\Delta i)}}{\sum_{k=1}^{4} e^{(-0.5\Delta i)}}$$

Confidence intervals for the growth parameters were estimated based on the likelihood profiles and chi-square distribution ($\chi^2$) (Venzon & Moolgavkar 1988). The confidence interval was defined as all values of $\theta$ satisfying the following inequality:

$$2(L(Y|\theta_{best} - L(Y|\theta_{best})) < \chi^2_{1,1-\alpha}$$

where: $L(Y|\theta_{best})$ is the negative log-likelihood of the most likely value of $\theta$, and $\chi^2_{1,1-\alpha}$ is the value of $\chi^2$ with one degree of freedom at the $1 - \alpha$ confidence level. Thus, the confidence interval at 95% of the value $\theta$ covers all values that are twice the difference between the log-likelihood of a $\theta$ given and the log-likelihood of the best estimate of a $\theta$ given on that is less than 3.84 (Haddon 2011).

If there is no best candidate model with an Akaike weight ($wi$) greater than 90%, an average model must be calculated as required when using the multimodel approach (López-Martínez et al. 2020). Once the best cases were determined and selected, it was possible to generate growth curves. We used the Kimura test (Kimura 1980) to analyze significant differences in the growth curves between males and females. The following formula was used:

$$X_k^2 = -N \times Ln\left[\frac{\sum RSS_i}{RSS_p}\right]$$

where: $k$ is the degrees of freedom (number of model parameters), $N$ is the total observations for both curves combined, $RSS_i$ is the total sum of squared residuals derived from fitting each curve separately, and $RSS_p$ is the total sum squared residuals derived from fitting the pooled curves. This analysis is performed only considering additive error.

## RESULTS

A total of 2719 snails of *Trochita trochiformis* were analyzed, 1763 females (64.84%) and 956 males

(35.16%). The sex ratio was 1.84:1 (F:M), and the goodness-of-fit test ($X^2$ = 237.478) showed significant differences between sexes ($P$ = 0.000). The average diameter and weight in females were 49.04 ± 5.79 mm and 36.27 ± 15.13 g, respectively, while in males, it was 44.81 ± 5.00 mm and 28.75 ± 11.00 g (Table 1).

The relationships of the $S_d - T_w$ variables for both sexes showed a potential-type relationship (Fig. 1). The allometry coefficient values for the population were $b = 2.61$, females $b = 2.60$, and males $b = 2.62$. For the three cases, the t-Student test indicated a negative allometric growth ($P < 0.05$). ANCOVA showed no significant differences in the relationship of $S_d - T_w$ variables between females and males ($P = 0.902$) (Table 2).

The Kolmogorov-Smirnov test, applied for $S_d$ data, showed differences between females and males ($Z$ = 6.4, $P$ < 0.001). It was observed that males show a higher frequency in smaller sizes between 40 and 50 mm $S_d$. In comparison, females have a higher frequency between 44 and 60 mm $S_d$ (Fig. 2). Comparisons between months for females of *T. trochiformis* showed differences in 71.5% of the 23 months analyzed, where January 2020 and March 2020 were significantly different compared to the rest of the months (Fig. 3a). In males, significant differences were found in 58.1% of the comparisons between months. Also, January 2020 and March 2020 differed from the rest of the analyzed months (Fig. 3b).

Box and whisker plots showed that during March 2020, females presented their largest $S_d$ range from 24.8 to 90.2 mm $S_d$ (range = 65.4 mm); however, the largest interquartile ranges were observed in January, February, May, June, and July 2020, and August 2021, showing greater $S_d$ variability (Fig. 3a). In males, also during March 2020, $S_d$ values from 8.13 to 92.6 mm (range = 84.47) were observed; with larger interquartile ranges, the months of December 2019, January and July 2020, and March 2021 showed greater variability in $S_d$ (Fig. 3b).

Multinomial analysis showed at most three modal groups for both females and males. In females, the three modal groups were observed in July 2020. The first group had an average $S_d$ of 8.11 ± 0.18 mm, the second group of 38.59 ± 2.22 mm, and the third group of 50.86 ± 5.50 mm. On the other hand, February 2021 also showed three modal groups. The first group with an average $S_d$ of 38.08 ± 0.51 mm, the second of 49.98 ± 3.48 mm, and the third of 59.70 ± 2.77 mm (Fig. 4). In the case of males, only March 2021 showed three modal groups. The first group had an average $S_d$ of 19.58 ± 3.53 mm, the second group 44.07 ± 6.06 mm, and the third group 63.59 ± 0.61 mm (Fig. 5).

The mean lengths of each modal group were plotted on a time scale, and we could identify up to 14 individual cohorts in both females and males (Figs. 4-5).

After fitting the modal progressions data (Table 3), case 2 was the best case for females ($wi$ = 0.39) and males ($wi$ = 0.53), demonstrating sigmoidal growth. In females, case 2 showed values of $\varepsilon(L_\infty)$ = 89.86 mm and an $a$ = 2.4; in males, the values were $\varepsilon(L_\infty)$ = 86.23 mm and an $a$ = 1.4. However, case 5 also adequately explains growth for both females and males according to the plausibility of $wi$ = 0.29 (females) and $wi$ = 0.21 (males) (Table 3). Cases 2 and 5 adequately describe the observed growth data for both sexes according to the difference in $AIC$ ($\Delta_i$) (Table 2). The resulting growth curves of cases 2 and 5 and the average model show that females have more accelerated growth. Females (88.04 mm) and males (86.23 mm) reach their maximum diameter at approximately 10 years; in both cases, the results of infinite $\varepsilon(L_\infty)$ obtained by case 2 are close to the $L_{max}$ observed in females (90.20 mm), and males (92.60 mm) (Fig. 6). The Kimura test for the estimated curves with the best case (case 2) showed highly significant differences between males and females of *T. trochiformis* (RSS = 571.68, $X_2^2$= 33.5, $P$ < 0.05).

## DISCUSSION

The $S_d - T_w$ relationship and the estimation of isometry showed a potential adjustment with negative allometric growth. It is not easy to compare the results because this type of study is rare in gastropod species since most have been more developed for bivalve species (Katsanevakis et al. 2007, Arce-Acosta et al. 2019). However, there are some works, such as the one carried out by Arias-López et al. (2022), in which the length-weight relationship in *Hexaplex nigritus* was estimated. They determined that *H. nigritus* presents a type of isometric growth, indicating that the species grows in the same proportion in length and weight. However, in the case of females and males of *T. trochiformis*, growth indicates that both males and females first grow in length, then increase in body weight; this could be related to seasonal changes, food availability, and species-specific physiological changes, such as age and sexual maturity (Ricker 1958).

The sexual proportion of the population of *T. trochiformis* was dominated by females, as previously reported by Ríos-Jara et al. (2004). In addition, the authors reported that organisms larger than 7 cm in shell diameter were exclusively female. In comparison, organisms larger than 1.67 cm and smaller than 7 cm

**Table 1.** Sampling months, number of organisms per sex, sample per month, ranges, and the average diameter and weight per sex and month of *Trochita trochiformis* in Puerto Vicente Guerrero, Mexico. F: females, M: males, n: sample size, Rsf: range sizes of females, Rsm: range sizes of males, afd: average females diameter, amd: average males diameter, awf: average weight females (g), awm: average weight male (g).

| Month | F | M | n | Rsf (mm) | Rsm (mm) | afd | amd | awf | awm |
|---|---|---|---|---|---|---|---|---|---|
| Oct-19 | 24 | 6 | 30 | 50-60.8 | 47-54.4 | 54.75 | 51.21 | 45.64 | 38.03 |
| Nov-19 | 20 | 10 | 30 | 43.8-58.7 | 35.5-54.2 | 51.36 | 41.21 | 40.09 | 21.91 |
| Dec-19 | 103 | 56 | 159 | 36.2-67.6 | 16.3-62.4 | 51.75 | 43.73 | 42.7 | 31.15 |
| Jan-20 | 54 | 34 | 88 | 57.2-87 | 45.1-78.5 | 68.69 | 61.49 | 96.41 | 71.94 |
| Feb-20 | 58 | 55 | 113 | 40.1-74.6 | 22-83.1 | 54.16 | 47.03 | 42.49 | 32.61 |
| Mar-20 | 60 | 86 | 146 | 24.8-90.2 | 8.1-92.6 | 36.6 | 35.1 | 14.31 | 13.01 |
| May-20 | 102 | 31 | 133 | 33.1-65 | 22.6-58.3 | 47.86 | 48.39 | 31.2 | 28.33 |
| Jun-20 | 90 | 25 | 115 | 38-81.3 | 35.1-67.2 | 53.27 | 48.67 | 46.55 | 36.5 |
| Jul-20 | 137 | 52 | 189 | 19.6-62.6 | 21.9-59.5 | 46.5 | 42.91 | 36.65 | 31.07 |
| Aug-20 | 82 | 47 | 129 | 19.3-65.3 | 21.3-60.5 | 50.11 | 46.27 | 36.96 | 28.81 |
| Sep-20 | 60 | 31 | 91 | 37.8-61.7 | 31.2-50.9 | 49.09 | 43.18 | 32.58 | 22.56 |
| Oct-20 | 102 | 35 | 137 | 30.1-60 | 33.5-54.8 | 44.43 | 42.8 | 31.44 | 26.76 |
| Nov-20 | 87 | 46 | 133 | 33.3-74.2 | 34.4-61.5 | 47.88 | 44.83 | 36.93 | 28.44 |
| Dec-20 | 85 | 53 | 138 | 32.8-60.2 | 4.3-58 | 49 | 46.42 | 36.47 | 31.23 |
| Jan-21 | 65 | 40 | 105 | 38.1-64.8 | 33.4-54.5 | 49.87 | 44.85 | 35.15 | 28.44 |
| Feb-21 | 88 | 46 | 134 | 36.9-64 | 36.7-60.8 | 50.89 | 46.34 | 37.45 | 29.82 |
| Mar-21 | 92 | 58 | 150 | 19.6-59.9 | 15-64.9 | 44.83 | 39.29 | 25.06 | 21.33 |
| Apr-21 | 118 | 22 | 140 | 32.3-62.2 | 37.4-55.2 | 46.47 | 43.8 | 28.39 | 23.98 |
| May-21 | 75 | 46 | 121 | 35.6-61.4 | 33.9-54.8 | 47.14 | 44.51 | 28.2 | 24.63 |
| Jun-21 | 68 | 46 | 114 | 34.8-56.5 | 24.2-53.2 | 45.9 | 39.52 | 28.55 | 18.75 |
| Jul-21 | 70 | 42 | 112 | 36.4-59.8 | 32.6-58 | 46.71 | 44.59 | 28.22 | 24.9 |
| Aug-21 | 49 | 25 | 74 | 32.4-65.3 | 34.1-77.5 | 44.41 | 42.46 | 24.43 | 26.46 |
| Sep-21 | 74 | 64 | 138 | 32.4-62.3 | 23.8-55.7 | 46.28 | 41.95 | 28.34 | 20.68 |
| Total | 1763 | 956 | 2719 | | | | | | |

showed a higher proportion of males. In the dominance of the females in the sexual proportion, we also observed that they had a greater mean size than the males (Fig. 2), which could significantly influence the higher proportion because *T. trochiformis* is a consecutive protandrous hermaphrodite that, during development, expresses an early male sexual phase, which would be related to the smallest shell diameters representative of age (Brown 1993). It has been observed that the change from male to female occurs at shell diameters greater than 3 cm (Bolvarán 1981). Therefore, since the organisms analyzed in our study come from commercial fishing, a large propor-tion of organisms above the average size for the start of sex change (3 cm) was observed, which could cause a bias towards a greater presence of females.

Calyptraeidae organisms that form large groups or associations within populations show greater variation in sex ratios. Collin (2006) analyzed the sexual inversion condition in 19 populations of different species of the Calyptraeidae family and concluded that the sex change in these protandrous species is directly related to density. We observed large groups of *T. trochiformis* during the sampling period in the study area. This characteristic observed in the analyzed population could be another reason the sex ratio showed differences in parity 1:1 (F:M).

On the other hand, the difference in the proportion biased towards females played an important role in the presence of similar sizes between males and females. As previously mentioned, males tend to be smaller than females due to their protandrous condition, so we expect to see this same pattern for *T. trochiformis* in Guerrero; however, both sexes showed similar sizes. This behavior is possibly related to the reproductive success of the males, which would generate slower growth, causing delay or variations in the size of change of sex (Brante et al. 2016), which could explain the presence of males of larger sizes. Munday et al. (2006) mentioned that a female-biased sex ratio could cause males not to change sex or only a part of the male population to change to females. Therefore, the female-dominated sex ratio of *T. trochiformis* in Guerrero could cause males to delay their sex change size, allo-

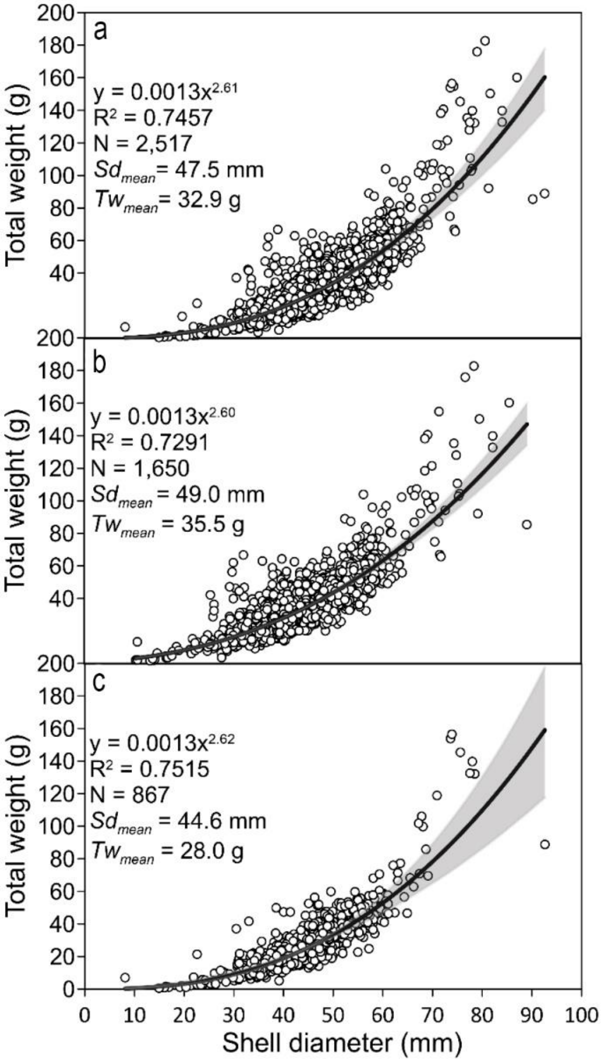

**Figure 1.** Diameter-weight relationship for a) the population, b) females, and c) males of *Trochita trochiformis* in Puerto Vicente Guerrero, Guerrero, Mexico. N: sample size, $Sd_{\text{mean}}$ and $Tw_{\text{mean}}$ are the mean shell diameter and total weight, respectively. Gray shading indicates confidence intervals.

wing them to reach similar sizes to females. However, further studies of the sex change behavior of this species must be conducted in the study area.

The multinomial analysis of *T. trochiformis* showed a total of 14 cohorts for males and females in two years of sampling, observing six to seven cohorts per year, a pattern similar to that was reported by Avila-Poveda et al. (2020) for *Chiton articulatus*, which showed two to three modal groups per month, and between seven and nine individual cohorts. The authors argue that the number of cohorts varies markedly as seawater temperature changes, increasing with higher mean annual temperatures (Culos & Tyson 2014).

Temperature variability is narrow in tropical environments (as in our study area). In Guerrero, there is a general variability of 3.1°C with ranges from 26.9-30°C, according to sea surface temperature data (Reynolds et al. 2002). In addition, the coastal region of Guerrero is characterized by high-temperature averages (García 1981). All this will cause continuous recruitment, allowing more cohorts per year. In this regard, Cárdenas & Aranda (2003) mention that in higher temperature ranges, recruitment is less continuous; therefore, the number of cohorts will be lower.

The number of cohorts is also related to reproductive biological aspects. In species of the Calyptraeidae family, it is common for gonadal maturity to be present throughout the year (Gallardo 1977, Deslous-Paoli 1985). This condition is probably related to the capacity of the females to store viable spermatozoa for long periods (Coe 1942), a condition that is expressed as a strategy in response to sessility and the short period in which individuals express the male phase, which, in some species of Calyptraeidae, varies between 6 and 24 months (Wyatt 1961, Hendler & Franz 1971, Deslous-Paoli 1985). In this regard, Cañete et al. (1993) determined that *C. trochiformis* from the Chilean coast produces egg mass throughout the year. This characteristic reproductive strategy of protandrous hermaphrodite species with direct development, such as *T. trochiformis*, guarantees more cohorts during an annual cycle.

According to Aragón-Noriega (2013), the most commonly used model in studies focused on estimating growth is the von Bertalanffy model. However, although being the most studied and commonly applied, its use as the only modeler of individual growth lacks proper support. Using a multimodel approach to describe growth is more viable since it allows us to model several hypotheses and, based on the $AIC$ quality indicators, facilitates the selection of the best model that fits the data. In other studies, in bivalve mollusks that determined growth using a multimodel approach, it has been observed that the Gompertz-type growth has been the one that best describes growth (Katsanevaskis 2007, Aragón-Noriega 2013). The present study found similar results since case 2 of the Schnute model is equivalent to the Gompertz model. Thus, this model described a sigmoid type of growth and was the best fit for the obtained data of *T. trochiformis*.

Sigmoidal growth describes an accelerated growth rate at early ages and decreases as the organism approaches adulthood (Iijima 2001). Some studies

**Table 2.** Student's t-test data was applied to determine isometry in females and males of *Trochita trochiformis* in Puerto Vicente Guerrero, Guerrero, Mexico.

| Sex | $a$ | $b \pm IC$ 95% | $R^2$ | $P\ test\ t\ (b)$ | $F$ (ANCOVA) | $P$ (ANCOVA) |
|---|---|---|---|---|---|---|
| Population | 0.0013 | 2.61 ± 0.05 | 0.75 | 0.003 | 0.015 | 0.902 |
| Females | 0.0013 | 2.60 ± 0.07 | 0.73 | 0.005 | | |
| Males | 0.0013 | 2.62 ± 0.08 | 0.75 | 0.008 | | |

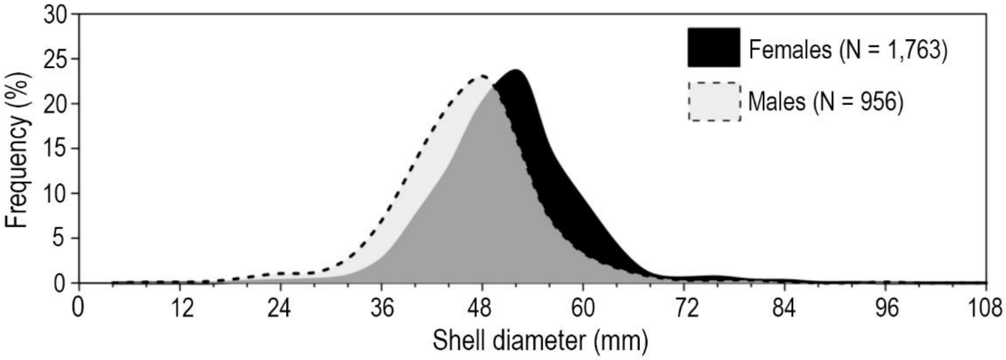

**Figure 2.** Size distribution of females and males throughout the study period. The Kolmogorov-Smirnov test indicated significant differences between both sexes.

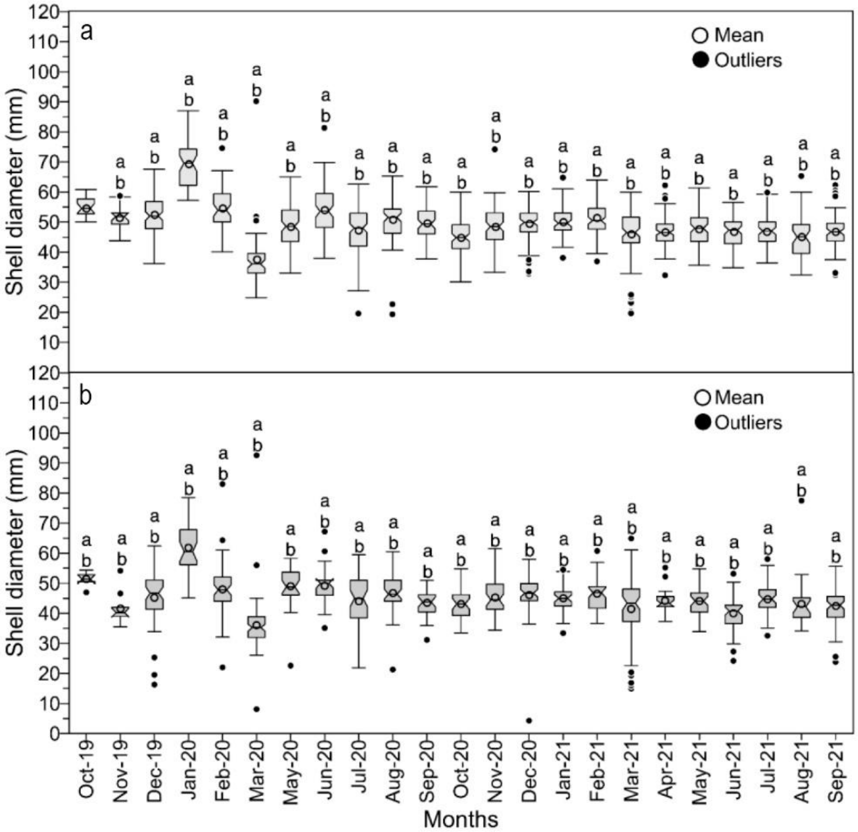

**Figure 3.** Shell diameter behavior in the different sampling months, represented in the box-and-whisker plot, a) females and b) males. The letter 'a' above shows significant differences between Jan-20 and all months, and the letter 'b' shows differences between Mar-20 and the other months.

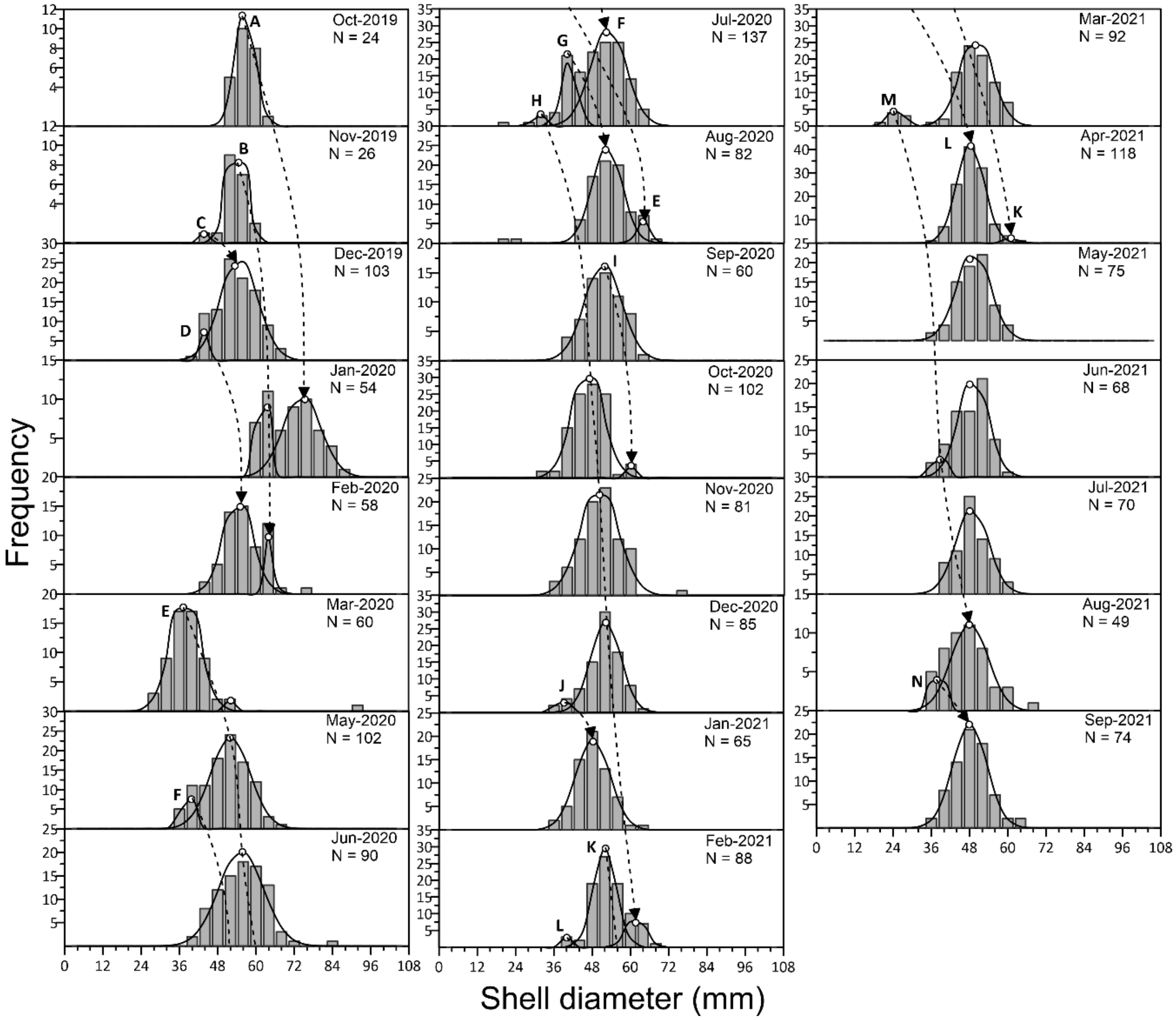

**Figure 4.** Monthly size frequencies (bars), modal groups (white circles centered on the curves), and modal progression of individual cohorts (labeled alphabetically according to their chronological order) for *Trochita trochiformis* females in Puerto Vicente Guerrero, Guerrero, Mexico.

describe that this behavior is directly related to seasonal changes in the reproductive cycle (Stoeckmann & Garton 1997); for example, in mollusks, larger organisms devote a greater amount of energy to reproduction during the summer rather than to growth (Stoeckmann & Garton 1997). *T. trochiformis* in the study region is influenced by the environmental characteristics of a tropical zone of the Costa Grande region of Guerrero, where warm temperatures are constant all year round (García 1981), which influences the reproduction of organisms throughout an annual cycle (Valdizan et al. 2011); in turn, this condition could reduce the growth rate. However, larger-scale events must also be considered, for example, during part of the study when there were cold event conditions (ENSO, La Niña, cool episode) (NOAA 2023), which caused an abnormal drop in surface temperature from the sea (SST), influencing and causing a reduction in the growth rate, a behavior similar to the one observed for the polyclacophoran *Chiton articulatus* in its tropical area of distribution (Avila-Poveda et al. 2020).

Regarding the type of growth in the curves generated from the best cases of the Schnute model and the average model, differences in growth between the sexes of *T. trochiformis* were observed (according to the Kimura test). Collin (1995) determined that, in *C. fornicata*, there is evidence that males grow faster than females of a similar size. However, the results in the present study evidenced that males of *T. trochiformis* showed a slower growth rate than females. This condition is probably related to sexual maturity since males mature faster, as reported by Brown (1989), who

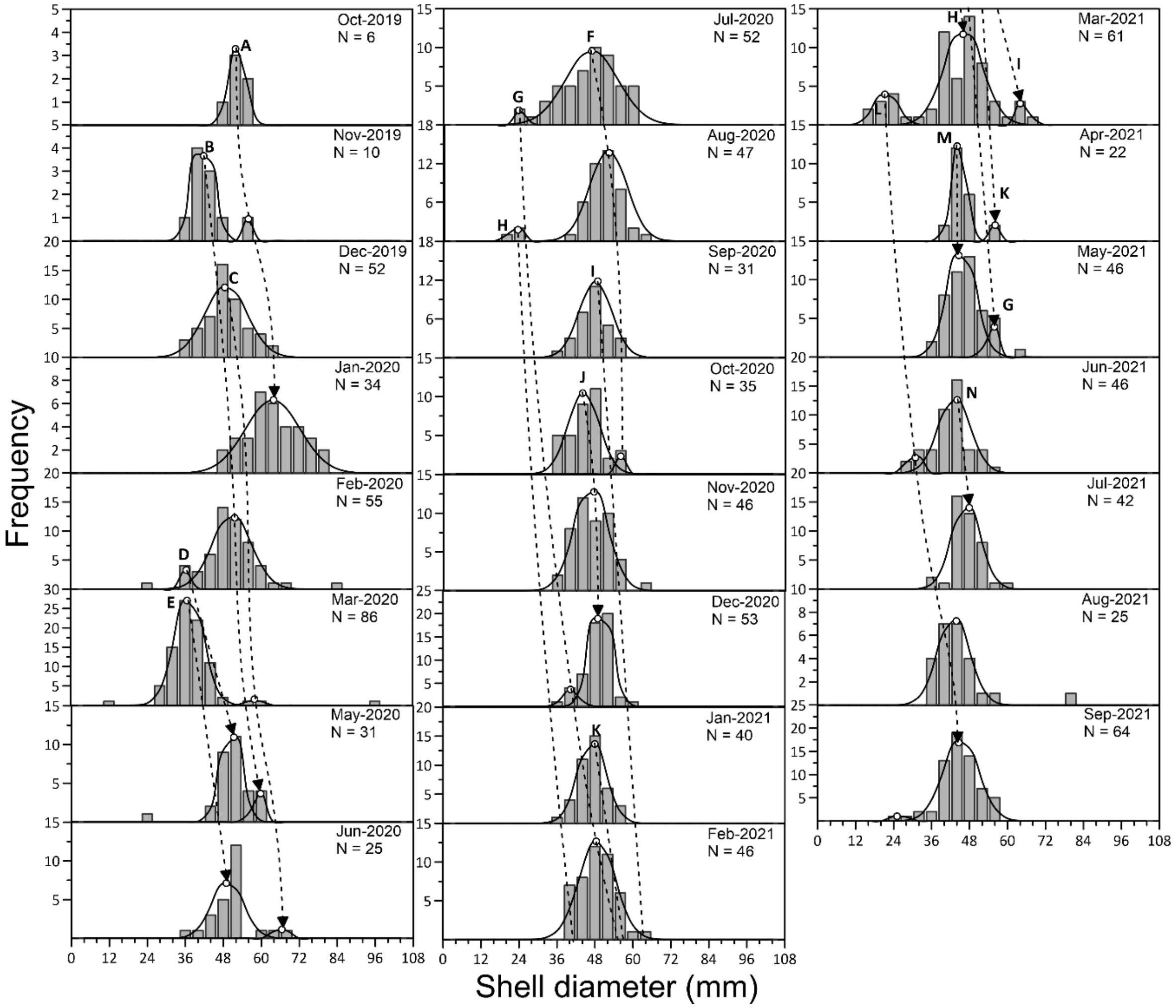

**Figure 5.** Monthly size frequencies (bars), modal groups (white circles centered over the curves), and modal progression of individual cohorts (labeled alphabetically according to their chronological order) for *Trochita trochiformis* males in Puerto Vicente Guerrero, Guerrero, Mexico.

describes that organisms of small sizes between 10-20 mm shell diameter are suitable for reproduction. The males analyzed were above the average size reported at the beginning of sexual maturity; therefore, we infer that the difference in growth rate between the sexes is because males concentrate all their energy on reproduction, not growth. Brante et al. (2016) determined that *Crepidula coquimbensis* males with more time in the copulatory position had lower growth rates.

The size advantage hypothesis predicts that reproductive output increases more rapidly with size or age in one sex than in the other (Warner 1975, Leigh et al. 1976). On the other hand, growth in females could be influenced by fecundity. In *T. trochiformis*, larger organisms produce more eggs; the size also affects the number of clutches a female can have in a year (Cañete & Ambler 1992). Therefore, the fact that female *T. trochiformis* grow faster than males could be because they focus their energy first on growth and then on reproduction.

In this study, *T. trochiformis* showed moderate growth because the organisms were captured in the rocky intertidal zone, an area exposed to strong waves. Another factor that could directly influence the growth of *T. trochiformis* is reported by Ríos-Jara et al. (2004), who determined that growth is related to the characteristics of the environment in which the species lives (Millán et al. 2000). Individuals with shell sizes greater than 3 cm in diameter that inhabit the upper mesolitoral zone in a protected area have a higher growth rate; on the other hand, organisms found in the exposed mesolitoral zone have a lower growth rate. The authors concluded that the difference in growth rate is due to the intensity of the waves and that the organisms use

**Table 3.** Quality estimators, growth parameters, and confidence intervals calculated for the five cases of the Schnute model estimated for *Trochita trochiformis* females and males. The best models are highlighted in bold.

| Model case | $AIC_c$ | $\Delta_i$ | $wi$ | $a\ (k)$ | $b$ | ε $(L_\infty)$ |
|---|---|---|---|---|---|---|
| | | | Females | | | |
| 1: $a \neq 0\ and\ b \neq 0$ | 114.9 | 2.6 | 0.10 | 3.42 (2.94-3.93) | -0.64 (-0.20 a -1.17) | 81.71 (75.1-88.9) |
| **2: $a \neq 0\ and\ b = 0$** | **112.3** | **0.0** | **0.39** | **2.40 (2.06-2.75)** | | **89.86 (82.2-98)** |
| 3: $a = 0\ and\ b \neq 0$ | 113.4 | 1.2 | 0.22 | | 1.49 (1.08-2.3) | 79.34 (71.3-87.2) |
| 4: $a = 0\ and\ b = 0$ | 128.2 | 16.0 | 0.00 | | | 3.72 (2.85-4.82) |
| **5: $a > 0\ and\ b = 1$** | **112.9** | **0.6** | **0.29** | **0.84 (0.73-0.97)** | | **129.68 (117.5-141.9)** |
| | | | Males | | | |
| 1: $a \neq 0\ and\ b \neq 0$ | 90.1 | 2.5 | 0.15 | 1.89 (1.76-2.03) | -0.48 (-0.29 a -0.69) | 79.17 (75.6-82.9) |
| **2: $a \neq 0\ and\ b = 0$** | **87.6** | **0.0** | **0.53** | **1.40 (1.31-1.50)** | | **86.23 (82.2-90.4)** |
| 3: $a = 0\ and\ b \neq 0$ | 90.8 | 3.2 | 0.11 | | 1.39 (1.27-1.55) | 50.78 (47.9-53.6) |
| 4: $a = 0\ and\ b = 0$ | 130.4 | 42.9 | 0.00 | | | 2.30 (1.97-2.67) |
| **5: $a > 0\ and\ b = 1$** | **89.5** | **1.9** | **0.21** | **0.41 (0.39-0.44)** | | **138.84 (131.4-146.2)** |

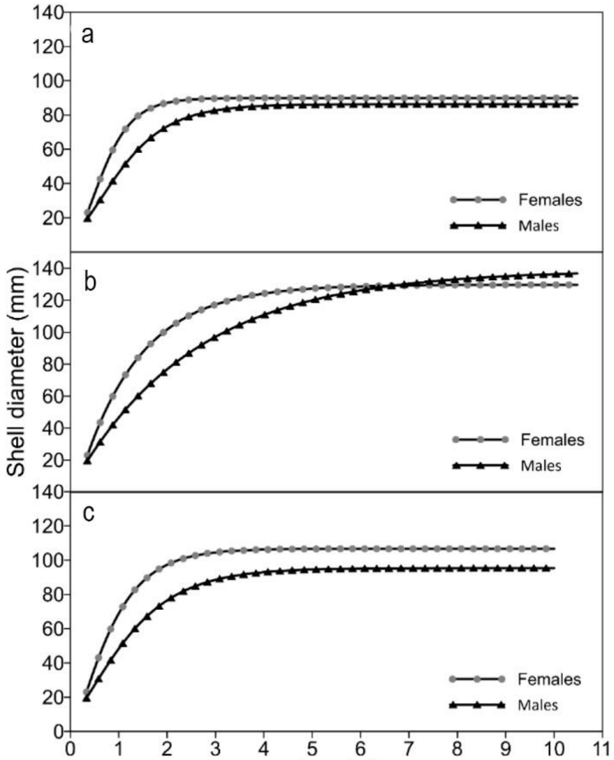

**Figure 6.** Growth curves of the best cases of the Schnute model for females and males of *Trochita trochiformis* in Puerto Vicente Guerrero, Guerrero, Mexico. a) Case 2, b) case 5, and c) average model.

the energy to stay attached to the substrate; thus, snails in protected areas will grow faster since they can use the energy for their growth.

It is important to highlight that males and females showed similar sizes, so subsequent studies should focus on evaluating the entire population. Several research steps would have to be followed, such as determining the gonadal stages of both sexes, estimating the average size at sexual maturity, and determining the maximum reproduction peaks (reproductive period); it is also essential to determine the copulation season and egg-laying season, as well as estimating abundance to know the availability of organisms accessible to fishing. On the other hand, if the fishery is based uniquely on females, future studies must consider evaluating the characteristics mentioned earlier for this sex. According to the available information, females reach larger sizes, so the minimum capture size could be established, considering the size at maturity. It would ensure that males (which are smaller) and females reproduce at least once, and the population is maintained. Castrejón-Ríos et al (2022) for *Hexaplex princeps* propose using the size at maturity of the females because in males this was smaller; this would protect both sexes. Another possible management measure is that catch quotas can be considered based on the abundance estimation, which would benefit *T. trochiformis*'s sustainability. Histological analyses are currently being carried out to determine the average size at maturity and reproductive period, and these results are expected to be published soon. This information and the data presented here will help with the main regulation measures for fishing *T. trochiformis* in Mexico.

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